CHRONOBIOLOGY, ECOLOGY AND BEHAVIOUR OF SOME INSECTIVOROUS BATS OF SOUTHERN INDIA

(With twenty-three text-figures and one plate)

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This review describes the experiments and results of our work with six species of insectivorous bats, inside natural caves, in open spaces and in the laboratory, performed by my students and me, in the Department of Animal Behaviour and Physiology, School of Biological Sciences, Madurai Kamaraj University in the two decades from 1975-1995. We had worked out in detail the behavioural expressions of biological clocks in four species of locally occurring insectivorous bats: *Taphozous melanopogon*, *T. kacchensis*, *Hipposideros speoris*, and *Rhinopoma hardwickei* and the activity/ roosting patterns of colonies of these bats in their habitat. Working at a depth of 40 m in a natural cave, we discovered that there is mutual social synchronisation of the circadian rhythm underlying the exodus flight of a colony of *c.* 600 *Hipposideros speoris* bats around the local sunset time. The circadian rhythm in the flight/rest activity of a solitary bat in a solitary cave without other conspecifics ('social informers') free-ran. We also report here results of experiments with *H. speoris* showing that daylight dimmer than starlight (0.0001 to 0.0006 lux) streaming into a cave for *c.* 90 mins could entrain their circadian rhythm. *H. speoris* is very sensitive to light, and light flashes lasting only 0.0625 msecs could shift the phases of the circadian rhythm. The spectral sensitivity of the photoreceptors in *H. speoris* indicates that they have colour vision. The Indian false vampire *Megaderma lyra* echolocates prey (frogs) by 'listening' to prey-generated noise on land (passive mode) and by active echolocation of the frogs in water (active mode). The eyes of most insectivorous bats are very small and are unlikely to participate in vision in the darkness of the night. It is suggested that eyes may participate in detecting dawn, sunrise, dusk and sunset, thus measuring daylength over the seasons of the year. There is annual breeding periodicity in *Hipposideros speoris*. There are 4 distinct breeding cycles in *Pipistrellus mimus*, the female giving birth to twins each time, making it the most prolific breeder among Chiroptera. Many of the observations reported here were first reports of their kind when they were made and published. The ecology of the day roosting sites, place fidelity and social interactions of insectivorous bats are fascinating facets that deserve to be investigated further.

INTRODUCTION

Bats, like rodents, are the largest group of mammals in the world with 1,001 species (Mickleburgh *et al.* 2002) and wide zoogeographical distribution. They can fly thousands of kilometres to inhabit remote islands in the Pacific and the Indian Oceans, live and flourish in all habitable regions of the earth. The Latin name for bats is Chiroptera which means hand-winged, as the forelimbs are modified into simple wings. There are two sub-orders: Microchiroptera (insectivorous bats) and Megachiroptera (fruit-eating bats). Microchiroptera are found in every continent except the Arctic and the Antarctic, whereas Megachiroptera (about 175 species, all belonging to one family Pteropodidae) are confined to Africa, Asia and Australasia. The fruit-eating bats have very large eyes and excellent eyesight, which helps them to find their way and their food in the dark; in contrast the insectivorous bats which rely almost exclusively on echolocation for navigation and foraging, usually have small eyes and very poor eyesight.

The world around us in the tropics is a fascinating place after sunset. There is swarming

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of myriad insects (mostly Lepidoptera, Diptera, Coleoptera and Orthoptera), the air has the fragrance of the flowers which open only at night to their pollinating agents, there is the alluring smell of ripening fruit too. This nightly world is the arena of bats, metaphorically called 'the birds of the night'. The insectivorous bats, without competition from birds, all of which (with a very few exceptions like nightjars and owls) are day active, crop the rich fare from this sea of insects on the wing. The power of flight and ability to echolocate prey are contributory factors for the evolutionary success of insectivorous bats.

G. Neuweiler (Zoologisches Institut der LMU, University of Munich) and his students and the dedicated group of bat researchers at the Department of Animal Behaviour & Physiology, School of Biological Sciences, Madurai Kamaraj University (MKU), Tamil Nadu, undertook a series of experiments related to field ethology, neurophysiology and chronobiology of nine species of echolocating bats of the Madurai region (9° 58' N, 78° 10' E). Neuweiler (1984) has summarised the findings of his team and reported that the insectivorous bats of Madurai foraged in three modes: 1) Surface gleaning, 2) Foraging within foliage, and 3) Open air foraging. Neuweiler elegantly demonstrated that the constant frequency/ frequency modulation (CF/FM) features and the bursts or train of 150 to 250 ultrasonic pulses per second emitted by the bat species while hunting, adaptively varied according to the mode of foraging and topographic features of the feeding habitat (Neuweiler 1984, 1990, Link *et al.* 1986, Marimuthu and Neuweiler 1987).

One of the most spectacular sights coinciding with the sunset in many parts of the world is the exodus flight of huge colonies of bats from their caves. In Bracken Caves in Central Texas, people assemble at sunset to see millions of free-tailed bats *Tadarida brasiliensis mexicana* stream upwards out of the cave for minutes on end. I noticed the same phenomenon when I accompanied my students to cave sites in Madurai when colonies of *Taphozous melanopogon, T. kachhensis, Hipposideros speoris, Tadarida aegyptiaca, Megaderma lyra* and *Rhinopoma hardwickei* flew out of their caves, evening after evening, within minutes of sunset, like cloudbursts. This 'emergence by coup' obviously is a collective behavioural expression of the perfect synchrony of the biological clocks of members of the bat colonies. This was the genesis of my interest in investigations on physiology of timing in various activities, chronobiology, and ecology of the insectivorous bats of Madurai. A study of the literature on the subject revealed that a few people had indeed reported a daily periodicity or circadian rhythm in insectivorous bats of Europe (DeCoursey and DeCoursey 1964, Erkert 1970, 1976, 1978, Laufens 1969, 1973, Voute *et al.* 1974) and the USA (Menaker 1961, Rawson 1960), the earliest of them being Griffin and Welsh (1937). Griffin had discovered the phenomenon of acoustic tracking of prey by insectivorous bats, and famously coined the term 'echolocation' (Griffin 1958). Most research effort in India on bats has been on taxonomy and embryology, contributions to the latter made mostly by M.A. Moghe, A. Gopalakrishna and colleagues (Gopalakrishna 1949, 1950, 1955; Moghe 1952, 1958). Therefore my students and I decided to concentrate on experimental studies of circadian rhythms, and field ethology observations on breeding cycles, ecology and the foraging strategies that these bats employ. There was no scientific information at all on biological rhythms of tropical bats in literature, except the observations of G. Neuweiler on the onset of activity in a colony of flying foxes in Madras (=Chennai) and dates of parturition (Neuweiler 1969). Brosset's papers (Brosset 1962a, b, c, 1963), first brought to my attention by Mr. J.C. Daniel, served as an excellent introduction to the bats of India.

The present review describes the experiments and results of our work, in the

laboratory, inside caves and in the open, carried out by my students and me from 1975 to 1995. We worked on the behavioural expressions of biological clocks in four species of locally occurring insectivorous bats: *Taphozous melanopogon*, *T. kachhensis*, *Hipposideros speoris* and *Rhinopoma hardwickei*, and have accumulated, as a result, the largest database on biological clocks of bats anywhere. This report includes data obtained in the laboratory on free-running flight activity rhythms in these bats and their responses to light pulses and monochromatic light pulses.

Terminology and Abbreviations

In the interests of readability, much of the jargon of 'chronobiology' has been left out of this essay. Some essential abbreviations and symbols, standardised by Aschoff *et al.* (1965), and since then much in use are given below.

LD: light/dark cycle

LL: continuous light

DD: continuous darkness

Circadian rhythm: daily rhythm with period close to 24 hours (Latin *circa* = about; *dies* = day).

Period: τ (tau): natural period of the circadian rhythm. In practice, time of onset of activity in LL or DD averaged over several days.

Entrainment: When environmental factors modify a circadian rhythm such that it has an exact period of 24 hours as it happens in nature.

Zeitgebers: Environmental cues (LD cycles for example) which entrain biological rhythms.

Free-run: State of the rhythm in LL or DD and constant temperature.

Phase: Any point along the circadian rhythm. Often expressed as CT (circadian time) denoting that it is not local time. (e.g. Sunrise = CT 0 hrs; Sunset = CT 12 hrs).

PRC: Phase response curve. Plot of the responses of a circadian rhythm, in terms of phase shifts, to perturbations (discrete displacements of the rhythm on time of day — X-axis) as a function of phase. (0° phase = CT 0 hrs; 180° phase = CT 12 hrs). Perturbations can be light, temperature, chemicals, social stimuli, etc. In this review, only light pulse PRCs are described.

Housing of Bats and Experimental Methods

Freshly captured bats that had been kept in the laboratory for close to a week, in a normally lit room, were used in the experiments. Our first problem was the capturing of the bats, but we soon became experts at catching them in fine mesh nylon mist nets. *Taphozous* spp. were the most difficult to capture.

Taphozous melanopogon: Body weight 20-24 g, best hearing frequency 26-28 kHz.

Field observations: This is a very common species and hunts high above the canopy in the open air. The field observations were made in the rock complex of the Jain Hills (Samanar Malai) in the vicinity of the Keela Kuyil Kudi village some 8 km southeast of the Madurai Kamaraj University campus. A colony of 150-180 animals of both sexes inhabited the vertical cracks and deep crevices of the rocks facing north. The bats crouched on all fours in clusters of 6-8 in the inner recesses of the crevices, some of them leading to dark, dank caves which progressively became narrow and inaccessible to observers. Older males and females often roosted in regions closer to the entrance, and were visible for observations during the daytime, often bathed in sunlight. Early observations lacked details about cluster size, sex composition, age distribution, hierarchical order, and exact numbers, for we had not yet acquired infrared viewers. Later observations by R. Subbaraj (unpubl.) confirmed the observations of Brosset (1962a) that the species was extremely polymorphic, variable in size and colour. Males were bearded. Later observations were made from comfortable perches, on a colony that lived in the outer yard of a temple 6 km west of the MKU campus on the banks of a bend in the Vaigai river.

Information on the various species of insectivorous bats of the Madurai region, location of cave sites, observing techniques of evening exodus flight of bat colonies, foraging areas and the bat lore could be obtained orally from the villagers living around the MKU campus. Bat counts were made during the onset of colony activity following sunset, the observer lying on a rock surface at the cave mouth and looking upward against the dimly lit dusk sky and counting the swift outward flight of the bats. In later studies, we used an infrared sniper-scope (FJW Industries, USA). Light intensity was measured during evening out-flight at the cave mouth using an AEG luxmeter and an optometer (United Detector Technology, USA). The lowest level of light intensity that could be directly and reliably measured with the luxmeter was 0.25 lux, but using the optometer on the energy scala scale we have measured 5% of starlight intensities (*c.* 0.0001 lux). Counting the bats when they returned to the cave was a more weary exercise, for each bat returned at its own time.

Captive bats were kept in the laboratory in 1 m x 1 m x 1 m wooden frame cages, wrapped around with nylon mosquito net, with a sleeve to put a hand in to feed the animals, change the drinking water, etc. Our German colleagues working in their laboratories, procured meal worm, commercially available in Germany, in abundance to feed their bats. Our meal worm was of very small size, so we resorted to feeding our bats on de-gutted cockroaches with elytra, wings, outer cuticle and legs removed. First the bats refused this unnatural fare but learnt to eat it after a sufficient build-up of hunger. They were always fed at night, and in later experiments during day into activity time, when we had offered the bats inverted light/dark (LD) cycles of 12:12 hours, with dark prevailing from 0800 hrs to 2000 hrs. Water with a few drops of Vitamin B-12 was available *ad libitum*.

Taphozous kachhensis: Body weight 48-54 g, best hearing frequency 24-26 kHz.

This is the largest and most sturdy species among the commonly occurring echolocating bat species in Madurai. It is as fast a flier as *Tadarida*, foraging at high speed (10-15 m/s) at heights of 17-30 m above the ground in unobstructed areas. A colony of these bats lived in the deep cracks and crevices of a rock complex called Pannian Malai, 5 km west of the MKU campus, not far from the road leading to Theni and Thekkady. The eyes of the bats were seen glistening during the day, when one peered into the cracks and crevices. The temperature in the inner recesses of the crevices was interestingly much cooler, at 27 to 28 °C, than outside where the temperatures could rise to 42 °C in the summer months. Both *Taphozous melanopogon* and *T. kachhensis* clung to the rock face on all fours. Unlike *T. melanopogon*, *T. kachhensis* was never seen roosting in temples or other human artifacts.

For experimental recording of the locomotor activity of both *T. melanopogon* and *T. kachhensis*, which did not fly within limited spaces but moved swiftly and laterally on all fours, we devised sturdy wooden tilting cages of 50 cm x 30 cm x 20 cm with a sliding door at one end and mesh net at the other. The cages were poised on knife edges and would tilt laterally, picking up the slightest ambulatory movements of the bats. The tilts activated the writing stylets of 20-channel A 620 X Esterline Angus Event Recorders (Esterline Angus Electronics Co., Indianapolis, USA). Experiments were performed in photographic darkrooms (chronocubicles) in desired DD, LL or LD conditions. Red light >630 nm was used to represent darkness ('safe light'). The temperature in the chronocubicles was constant at 28 ±1 °C and the relative humidity was artificially raised to 60 to 65% for experiments with *Taphozous melanopogon* and *T. kachhensis*.

A small colony of 25 *Taphozous kachhensis* bats comprising both sexes was maintained in an outdoor bat enclosure of 7.5 m x 3.0 m x 3.75 m with a fishpond of dimensions 4.15 m x 2.39 m x 0.64 m filled with water. Frogs in good numbers

were introduced into this pond. The water in the fishpond helped to increase the relative humidity inside the enclosure. The sides of the enclosure were limited on all four sides, by walls 2 m high and the enclosure was roofed over by steel rods forming a grating, which permitted the air movement but was too restrictive for the bats to fly or squeeze out. The enclosure was in the midst of a mango grove in the Botanical Garden. A row of *Polyalthia longifolia* trees on the east side of the enclosure, and mango trees on all sides, provided shade in the early morning hours. At the east end of the pond was a dark wooden enclosure in which bats roosted during daytime. The humidity varied from 35 to 65% and the temperature from 22 to 30 °C. This outdoor bat enclosure was our own idea and the outfit came in handy for the 'Prey capture by the false Indian vampire bat' experiments (Habersetzer and Marimuthu 1986, Marimuthu and Neuweiler 1987) and for video recording flight patterns of our bats. The onset of flight activity following the sunset and end of activity of the group of captive *T. kachhensis* bats were monitored for a whole year from January 1979 to January 1980. These bats flew around and fed on insects attracted to a mercury lamp (125 W) mounted within the enclosure. The bats drank the water from the pond.

Hipposideros speoris: Body weight 6.5-7.0 g, best hearing frequency 137 kHz.

This bat typically forages close to the canopy, around bushes and trees and very close to obstacles. A colony of 550-600 bats inhabited a true cave, which was 40-45 m deep in some of its pockets, in the Jain Hills. Actual observations of emergence flight of bats and their return were made at this site (Marimuthu 1984). In a nearby cave, which was more a hollow in a rock-front, lived a much smaller colony of *c.* 50 bats of *Hipposideros bicolor fulvus.* The mortality after capture of these bats was so high that it was decided that G. Marimuthu and Dilip Joshi would work with the sturdier *H. speoris.* As a result, we have accumulated a wealth of information about the biology, behaviour and circadian rhythms in this species. These bats also lived for long periods of time in captivity in good health.

Freshly caught bats were brought to the laboratory and placed in a 1 m x 1 m x 1 m nylon mosquito mesh cage for a week to allow them to acclimatise to the laboratory conditions. These bats spaced themselves out without ever clustering. In fact, each male bat had his 'personal' space, inside the cave as well as in the laboratory, which he would defend from intruders. The average space between two neighbouring male bats was 18 ±3 cm (n=12 observations on 46 animals) (Selvanayagam and Marimuthu 1984). Females seem to choose their roosting position in relation to males. Males, in addition to urine-marking their personal space, also adhere to a strict hierarchy in their roosting (Chandrashekaran, unpubl.).

For the experiments, the bats were brought into the chronocubicles and housed in flight activity cages of dimensions 30 x 30 x 30 cm, one bat in one cage. The cages had light aluminium frames and were covered with mosquito mesh netting and suspended from firm arms of tripod stands with strips of spring. *H. speoris* bats resorted to brief bursts of sustained flight and such activity jiggled the cages. The vertical oscillations and displacement of the cages depressed microswitches activating the stylets of Esterline Angus Event Recorders.

In the cave experiments performed by my students, G. Marimuthu (from 1978 to 1983) and Dilip Joshi (from 1980 to 1985) the same actograph (activity recording device), as described above, was used, employing a hand-wound Lambrecht-KG-Göttingen thermohygrograph instead of the electricity-run Esterline Angus Event Recorders. The thermohygrograph completing one revolution in 24 hours was adopted for tracing activity/rest patterns by writing ink stylets fixed on the flank of activity cages. The sturdy set-up, shown in Plate 1, Fig. 1, was placed 40 m deep into the cave. The activity/rest patterns of three bats

Chandrashekaran, M.K.: Thermohygrographs PLATE 1

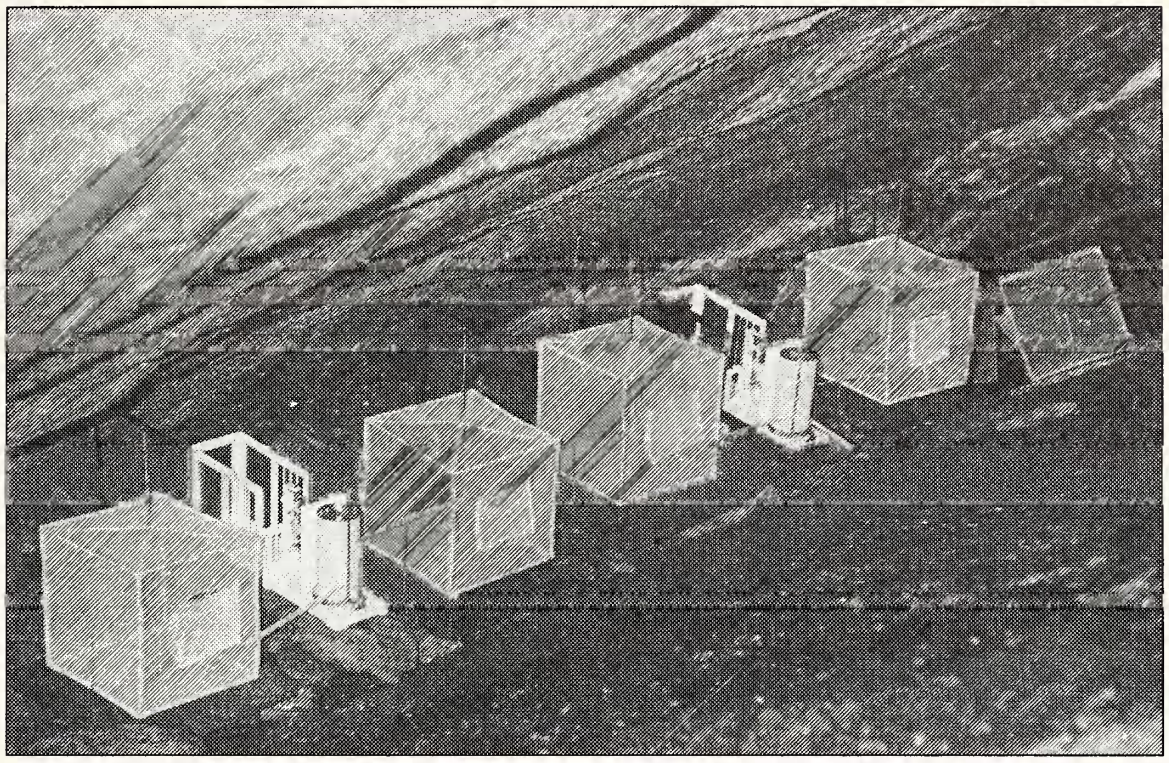


Fig. 1: The experimental set-up of suspended flight activity cages and hand-wound thermohygrographs

Fig. 2: Thermohygrographs placed in different parts of the *Rhinopoma hardwickei* cave

could be simultaneously traced, the longest experiment lasting up to 60 days. The ambient temperature in the chronocubicles was 28 ±1 °C and relative humidity was maintained high at 85 ±5% (since the relative humidity in their cave is 90% or higher).

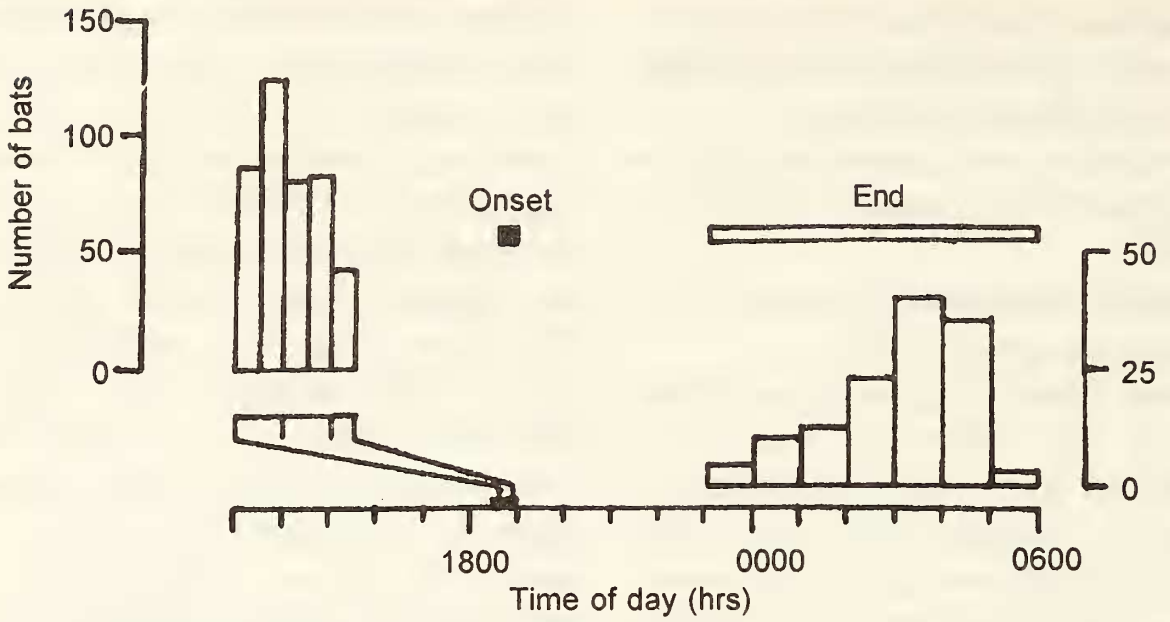
Rhinopoma hardwickei: Body weight 14-15 g, best hearing frequency 35 kHz.

Rhinopoma hunts flying insects at medium heights of up to 10 m above the ground and always keeps away from dense background. A stable colony of *c.* 1,500 bats of both sexes of the mouse tailed bat *Rhinopoma hardwickei* roosted in a narrow cave with high ceiling in the western flank of the Nagamalai Ridge, which forms the backdrop to the MKU campus. The population was intensively studied (Usman *et al.* 1990) for emergence and return flight patterns from August 1978 to August 1979. Additional observations were made during the period January to December 1980. The temperature and relative humidity in the various pockets of this irregular cave were measured using thermohygrographs. Wind conditions were recorded with a portable wind meter (Lambrecht KG Woelfle type) erected on a tripod stand in the study area. Sunrise and sunset times for all our field experiments were obtained from the Indian Ephemeris Nautical Almanac published by the Director of Observatories, Kolkata and were adjusted for latitude, longitude and Indian Standard Time. No laboratory experiments were performed either with *Taphozous kachhensis* or *Rhinopoma hardwickei.*

Results of Field Ethology and Laboratory Studies

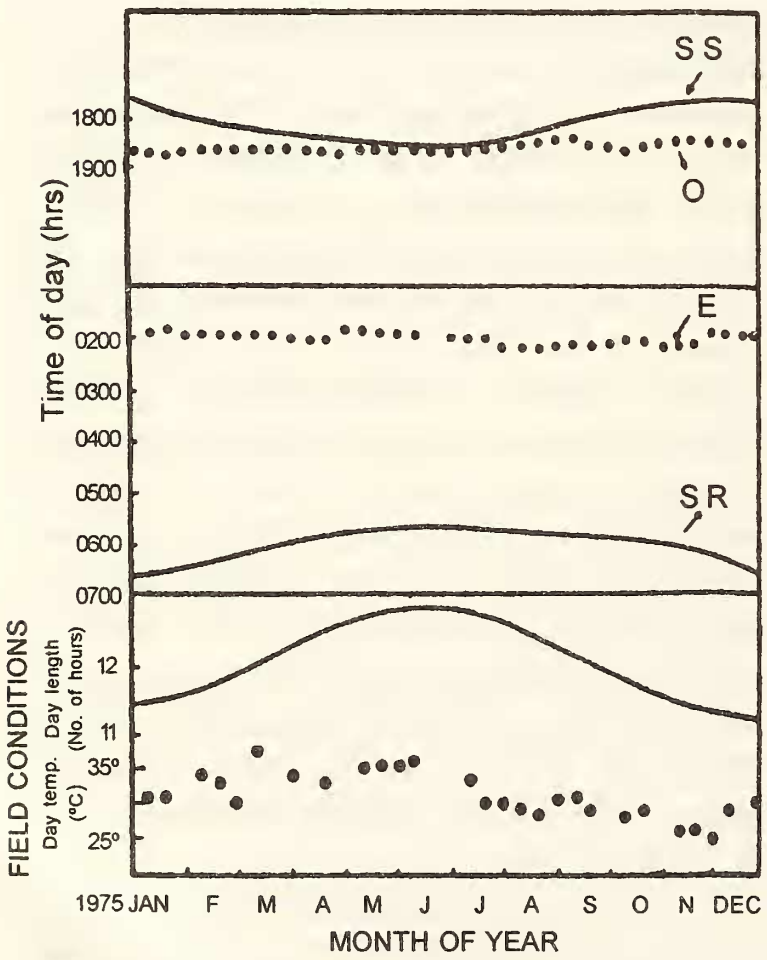
Activity and roosting patterns of a colony of *Taphozous melanopogon*: Voute *et al.* (1974) and DeCoursey and DeCoursey (1964) had observed that members of their bat colonies of *Myotis* spp. crowded at the entrance to their roost before flying out in the evenings to forage. In Germany, Rudolf Rübsamen and Michael Eckrich, who had each spent a few weeks and a whole year respectively at MKU, took me to the countryside churches in Upper Bavaria to see huge colonies of *Myotis myotis* roosting there. At sunset, these bats came to ledges from where they appeared to be 'sampling light' for close to 40 minutes in the long twilight of the higher latitude, before taking off. Such 'light sampling' behaviour could not be established for *T. melanopogon.* On the other hand, these bats appear to be exposed to the ambient light all through the day and could perceive nightfall, which came in a matter of 6 to 8 minutes in Madurai, directly. The time of the first flier could be generalised as the exact time of onset of foraging flight activity of the colony, for hordes of bats followed within seconds in clusters of 6 to 8. These observations were made at intervals of 10 days during January 1975 to January 1976. The difference between the longest and shortest days in Madurai is well below 2 hours. The entire colony empties out within 18 to 21 minutes, indicating great inter-individual synchrony in onset of activity but *not* in its termination, as shown in Fig. 1. Even though the time of sunset during the course of the year varied over a range of 41 minutes, the bats showed astonishing rigidity in the time of their emergence which was restricted to a narrow 'gate' of 16 mins, where the first bat emerged between 1825 hrs and 1841 hrs. The onset of foraging flight of the first 'sentinel' bat under field conditions, plotted against the months of the year, is illustrated in Fig. 2. Each dot of the 2 sets of 36 dots represents single observations on the 'onset' and 'end' of the activity of the bat colony made at 10-day intervals from January 1975 to January 1976.

The precise timing of emergence of the bats is well illustrated by the following incident. Eberhard Gwinner (Director MPI for Behavioural Physiology, Andechs, Germany) was visiting me in 1977 and wanted to see for himself this great precision in the onset of the outward foraging



■ = Time taken for first bat to last bat to emerge (mere 22 minutes)
▭ = Time taken for return flight (spread over 6 hours and 14 minutes).

Fig. 1: Pattern of 'onset' and 'end' of the nightly foraging flight of members of a colony of *Taphozous melanopogon* (After Chandrashekaran *et al.* 1983). Actual numbers flying out and returning do not tally since the bats took different routes, especially during the onset of foraging flight.



O = Onset of activity, E = End of activity.
SS = time of sunset, SR = time of sunrise.

Fig. 2: Field data of flight activity of *Taphozous melanopogon* bats (After Subbaraj and Chandrashekaran 1977)

activity of the colony. We took him to the site. Gwinner lay on a rock facing the crevices and was impatiently looking at his watch and called out at 1826 hrs, "Where are your bats?". The exodus started within seconds of the question and Gwinner was greatly impressed.

The timing of end of activity was imprecise in all seasons. The narrow gate in the timing of emergence flight implies that there is a seasonally changing threshold in sensitivity to twilight. Thus bats began flying when it was very dark on short days (0.1 lux) and flew out in sunlight even as the sun was going below the horizon (50 lux) on long days. It is unusual for a nocturnal mammal not to have a reasonably definable and fixed lower light intensity as a trigger to nightly activity, and therefore our findings need to be further investigated. Our findings are also at variance with the observation of Brosset (1962a) on *Taphozous melanopogon*, "The nocturnal outings of the colony take place 25 to 30 minutes after sunset (Kanheri and Mandu)". But Brosset, of course, as he himself has pointed out, did not make a systematic year-round study of these phenomena.

Werner Siefer, a project student of G. Neuweiler, who was visiting us in 1990, declared one day that he had seen bats 'soaring' at heights of *c.* 200 m soon after sunset. My response was that it was not possible for bats to soar. Textbooks tell us that bat wings are designed for flapping flight. "To stay airborne, a bat requires 8-15 wingbeats" (Neuweiler 2000). R. Subbaraj was requested to look into the matter. He accompanied Siefer with a pair of powerful binoculars. It was a warm full moon evening and it had drizzled. The bats were indeed soaring 150-200 m above the Jain Hills rock formation (Siefer and Kriner 1991). R. Subbaraj identified the species as being probably *Taphozous kachhensis*. The bats were apparently soaring in the thermal layer arising from the rocks below and cropping a rich fare of insects. Unfortunately, this interesting phenomenon was not further investigated, since both Werner Siefer and Eva Kriner left for Munich soon after making the discovery. It makes sense to assume that these bats had switched off their echolocation system while soaring, and the insects would have been plentiful anyway. They just had to soar with their mouth open and close it with a mouthful of insects.

Activity and roosting patterns of a colony of *Hipposideros speoris*: The observations on onset and end of activity were made at fortnightly intervals from December 1977 to January 1979. It was possible to count bats flying out in the twilight, against the still blue sky. The time of emergence of the first bat was recorded, and thereafter the number of bats emerging every minute was counted for as long as the prevailing twilight permitted. Light intensity was measured during the evening out-flight at the cave mouth, using the optometer with the photosensor pointing to the zenith.

Prior to emergence, approximately an hour before sunset, bats become restless and exhibit circular scanning head and ear movements, wing flapping, elaborate autogrooming, rocking forward and backward, and brief stretches of flights. The ear and head movement, noticed through the noctovision apparatus, may just mean that these bats were echolocating our presence in the total darkness of their roosting site. The commotion inside the cave gradually builds up, but since adults of *H. speoris* are "silent" and only produce ultrasonic pulses of 134 kHz, in this case there is none of the noisiness associated with the onset of colony activity in bats of other species. Flying around of the bats also intensifies the smell of bat guano inside the cave. When the light intensity steeply decreases during sunset, bats fly farther and farther toward the entrance of the cave. Bats of both sexes live in the innermost recesses of the cave. The darkness in the deeper parts is absolute and 1000 seconds exposure of the photoelement of the optometer on the energy scala scale did not register any light. About 10 to 20 minutes after sunset, in all seasons, a solitary bat invariably darts out of the cave to return immediately. We have never been able to verify if it was the same 'alpha' bat that emerged every evening and banding the bat did not help. A little before exodus, the entire colony of bats remain milling around very close to the cave mouth 'sampling light' (Twente 1955), then groups of 10 to 15 bats break off and fly into the night sky. However, on any given night, about 3 to 5% of the bats remained inside the cave. It was not possible to determine the returning time with any degree of accuracy, since bats flew in and out throughout the night. Further, bat mothers returned frequently to check if their pups were safe, when they did not carry them to the foraging sites. Evening departure of bats usually occurred at low twilight intensities that ranged over the seasons from 4.5 to 40 lux. Fig. 3 summarises the findings on *H. speoris* (Marimuthu 1984). It is clear from the figure that the onset and end of colony activity systematically changed and remained close to the timings of sunset and sunrise, respectively.

Fig. 4 illustrates the pattern of emergence flight of the colony of *H. speoris* made on four nights, in December 1977 (short daylength), March (neutral daylength), June (long daylength) and

October 1978. The bat counts were made every minute and shown here added up for five minutes. The pattern of scattered emergence on the night of June 23, 1978 might have resulted from the frequent outward and inward flight of suckling bat mothers. Fig. 5 is a representative example of

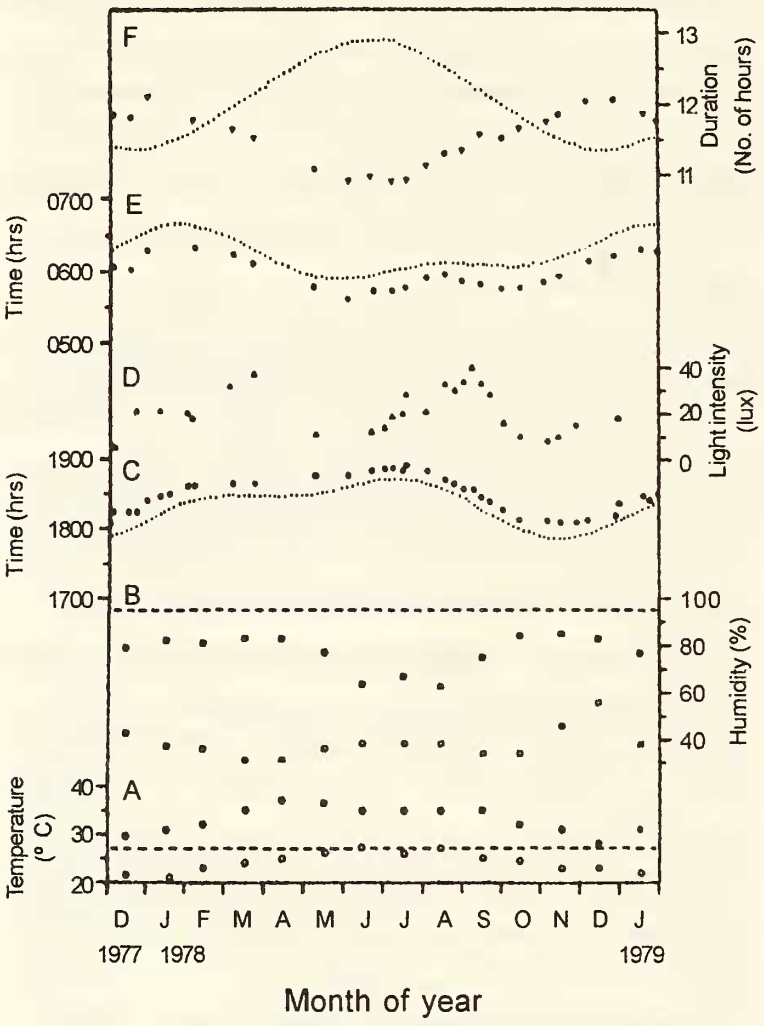


Fig. 3: Summary of the nocturnal activity pattern of a colony of *Hipposideros speoris* for the period of a year (After Marimuthu 1984)

Key to panels:
A: Temperature variations at time of onset of activity. Upper (solid) circles = temperature maxima, lower (open) circles = temperature minima, broken straight line = remarkably constant temperature of 27 °C inside the cave.
B: Maxima and minima of humidity.
C: Sunset (dotted line) and onset of colony foraging flight (solid circles).
D: Light intensity.
E: Sunrise (dotted line) and end of colony activity (solid circles).
F: Relationship between daylength (dotted line) and duration of activity (solid circles).

end of activity of the colony where numbers build up with approaching sunrise and terminate abruptly. The precision in the timing of onset and end of activity over various seasons in the colonies of insectivorous bats has been reported by many authors (DeCoursey and DeCoursey 1964, Erkert 1976, 1978, Griffin and Welsh 1937). The actual onset of exodus in *Hipposideros speoris* is preceded by arousal, which is obviously accomplished by the endogenous circadian rhythm acting like a wake-up timer. The light sampling is actually employed to fine-tune the circadian clock. A bat that tries to fly out before its time is exposed to bright light, which causes the clock to delay its functioning. Similarly, a bat that does not return to its cave early enough would be exposed to the bright light of the rising sun. A light pulse shock, at that phase in the animal's clock, 'advances' the phase. These discrete phase delays effected by light during sunset, and discrete phase advances effected by sunrise, explain how the bats do not fly about at unusual hours in nature. This tuning of the biological clocks by light is called entrainment (Aschoff 1960, Pittendrigh 1960).

Activity time: Marimuthu (1984) has made a fine structure analysis of the seasonal changes in the precision of the onset and end of the *H. speoris* colony activity under natural photoperiodic conditions. The duration of activity of the colony was measured as the time elapsed between the flying out of the first bat and the return of the last bat. The duration of activity followed the seasonal changes in the photoperiod, being longer over shorter daylengths and shorter over longer daylengths, indicating a positive correlation between the duration of colony activity and the length of night (Fig. 6). Fig. 7 represents the regression analyses of the timings of sunset and emergence of the first bat, and Fig. 8 represents the regression analyses of the timings of sunrise and return of the last bat, over the seasons. The lower light intensities triggering the onset of colony activity

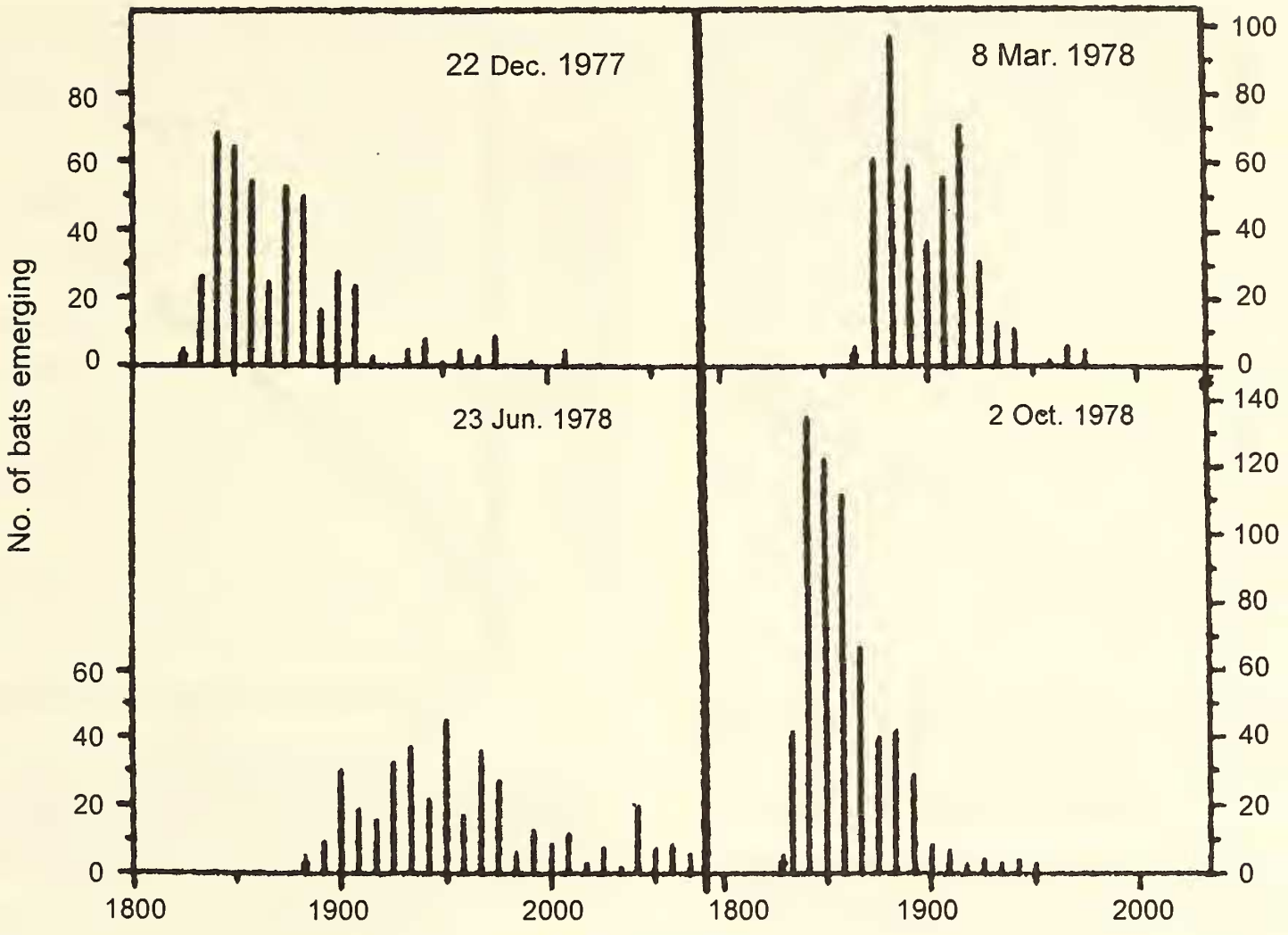


Fig. 4: Representative examples of the pattern of emergence of members of the colony of *Hipposideros speoris* (After Marimuthu 1984)

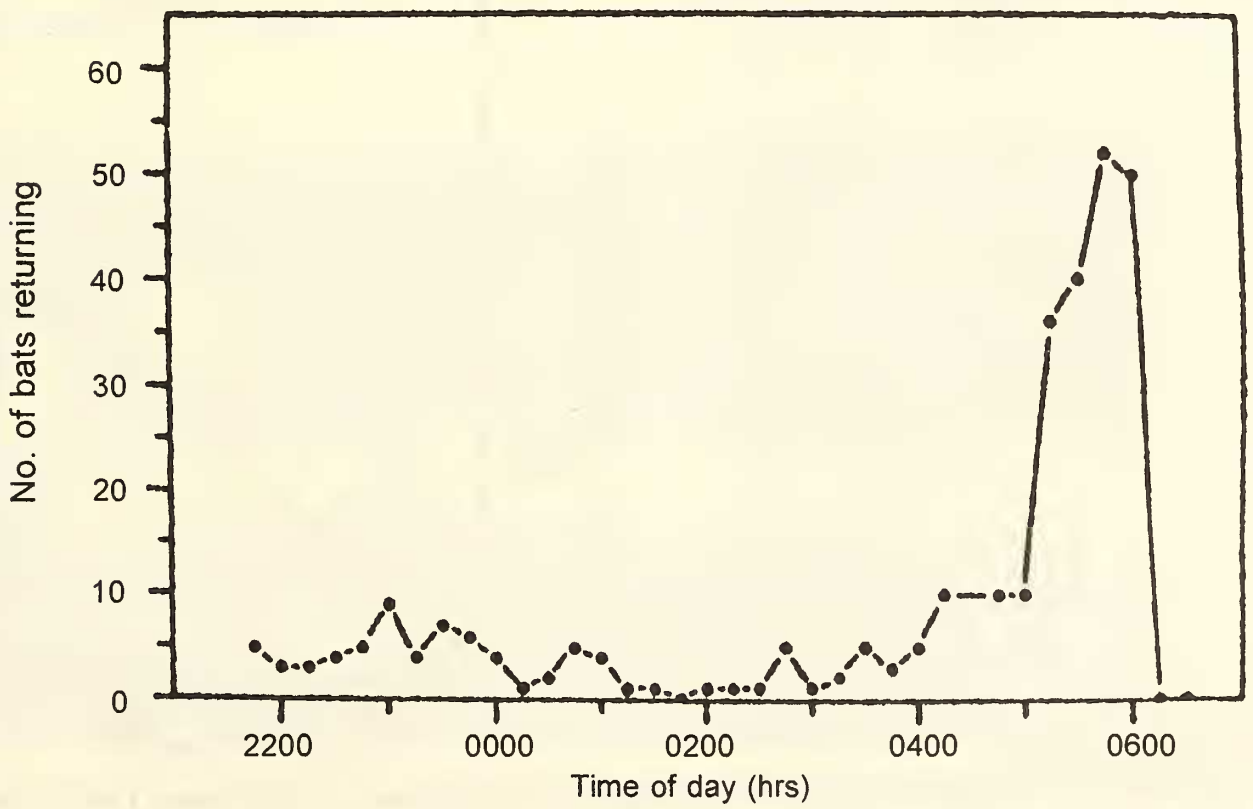


Fig. 5: Representative pattern of return of members of the *Hipposideros speoris* colony over the course of an entire night (After Marimuthu 1984)

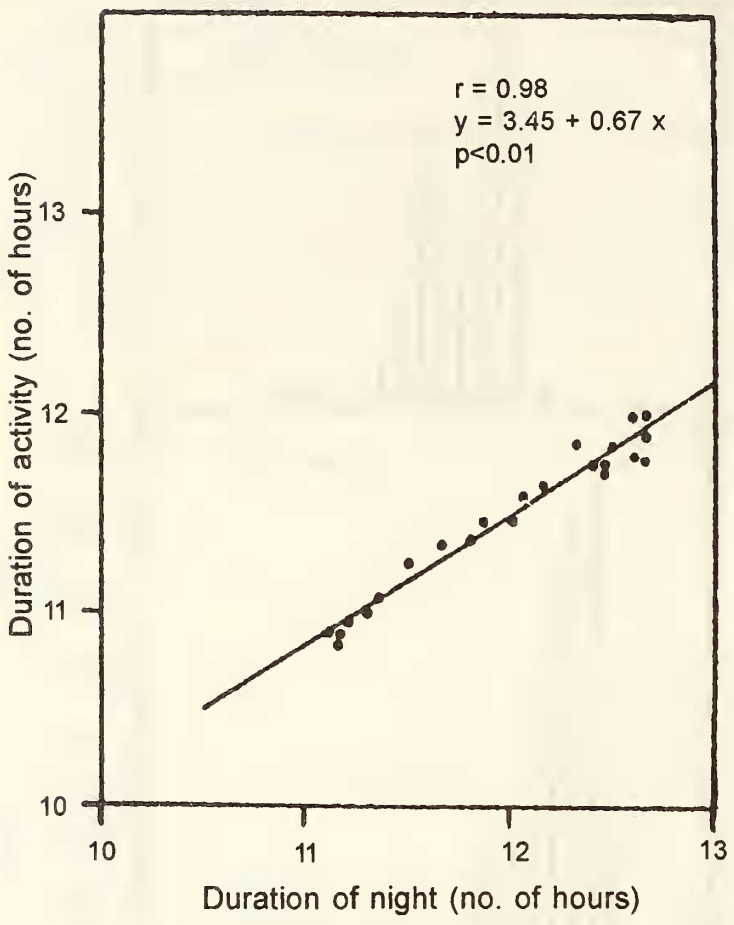


Fig. 6: Correlation between activity period of *Hippositleros speoris* and duration of night (After Marimuthu 1984)

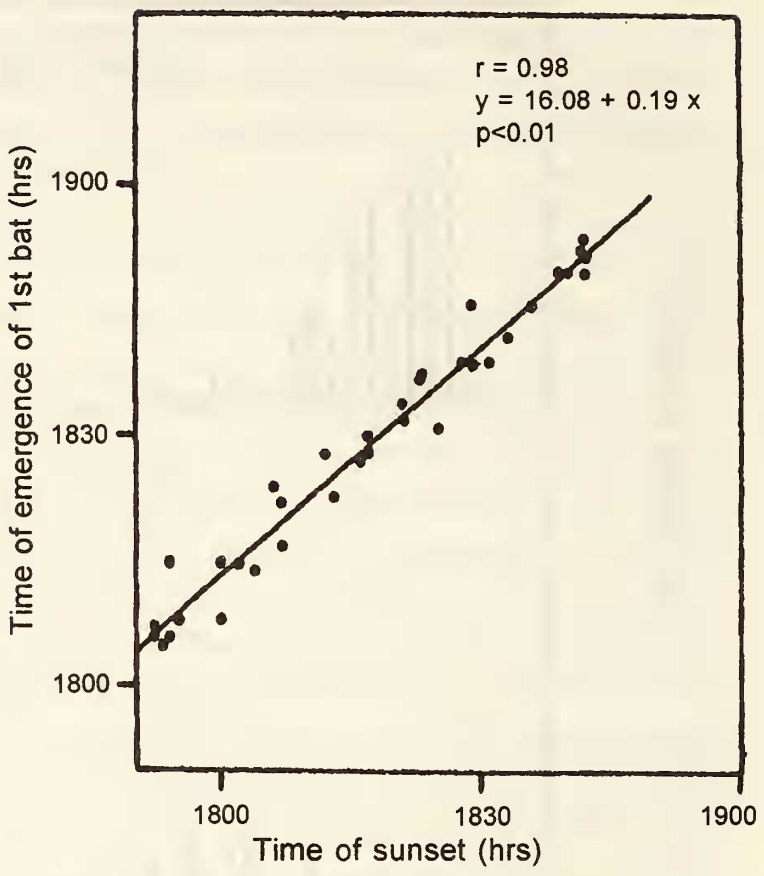


Fig. 7: Linear regression of time of emergence of the first *H. speoris* bat of the colony in relation to the time of sunset over the seasons (After Marimuthu 1984)

varied marginally over the seasons, indicating that there is no fixed lower threshold. The rate of change of light intensities during the brief dusk and dawn appears to be the primary and reliable environmental cue for these bats to modulate the onset and end of activity. It was not possible to precisely determine the beginning of return flight, because the bats indulged in both inward and outward flights sporadically during most of the night. By around 0300 hrs, the flight was essentially back to the cave and the build up in numbers was impressive an hour before sunrise. At this time the bats did not dash into the cave but undertook circling flights near the mouth of the cave at an altitude of one or two metres. The precise function of these manoeuvres is not clear, but it has been understood by us that the bat was daily fortifying its place memory. The bats then ceased to emit the trains of ultrasonic pulses and literally dived into the cave. These findings on activity duration, onset and end, relative to the

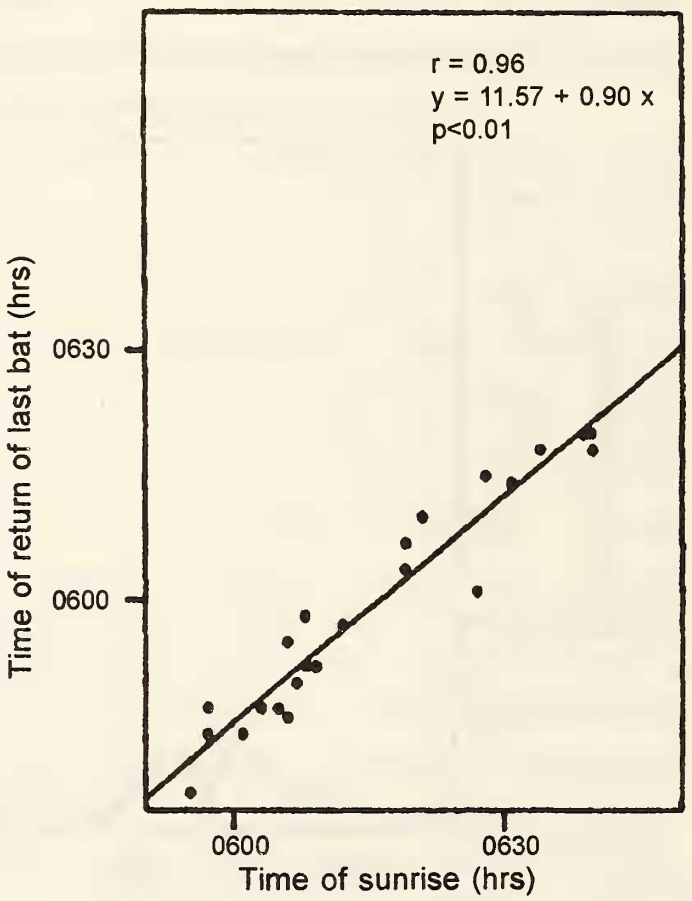


Fig. 8: Linear regression of the time of return of the last *H. speoris* bat of the colony in relation to the time of sunrise over the seasons (After Marimuthu 1984)

daylength (photoperiod) are in accordance with the rules formulated by Aschoff (1960, 1969) for diurnal and nocturnal animals, known as Aschoff's Rule (Pittendrigh 1960). Marimuthu's (1988) studies of these parameters in *H. speoris* were the first of their kind on a tropical bat species.

Activity and roosting patterns of a colony of *Rhinopoma hardwickei*: A number of caves, caverns and crevices that accommodate bat colonies exist in the Nagamalai Ridge. There, we decided to study a colony of *Rhinopoma hardwickei* which in many ways was different from *Hipposideros speoris.* The first feature I noticed was that there was an unmistakable smell, and that the members of the colony were found in all parts of the cave and roosted in different parts of the cave at different hours of the day. There certainly was nothing like 'personal space' or a marked hierarchy. These bats have two kinds of roosting positions, either resting on all fours like *Taphozous* spp. or hanging free like *Hipposideros* spp. The cave was more like a crevice and its topology is shown in Fig. 9. During field observations I noticed that most bats of the colony were close to the spacious high-roofed (*c.* 7.2 m) cave mouth which faced the west, in the cooler hours of the morning. The bats frenetically waved their prehensile and longish tails by means of which they detected and crept into narrow cracks in the wall of the cave. Plate 1, Fig. 2 shows the thermohygrographs placed at different positions inside this cave. With the help of special, elongated thermal probes, we could measure the temperatures prevailing in nooks and corners. The bats roosted in big clusters of 30-40 animals and the clusters moved progressively inwards in the cave, which was very dark and very cramped — in places, less than 1 metre wide — for the observer to position himself. By evening they had all crouched in inaccessible recesses and cracks in the inner walls of the cave. Careful measurement of the ambient temperature at the sites in which they roosted indicated that the bats were moving to zones of constant temperature of 27-29 °C. A rough sketch about how a cluster of bats moved on a hot May day is shown in Fig. 10. In *R. hardwickei*, constancy of temperature of *c.* 27 °C was possibly being sought by the bats rather than absence of light. This might also be the situation with *Taphozous melanopogon* and *T. kachhensis,* with none of the three species having well-marked 'personal space'.

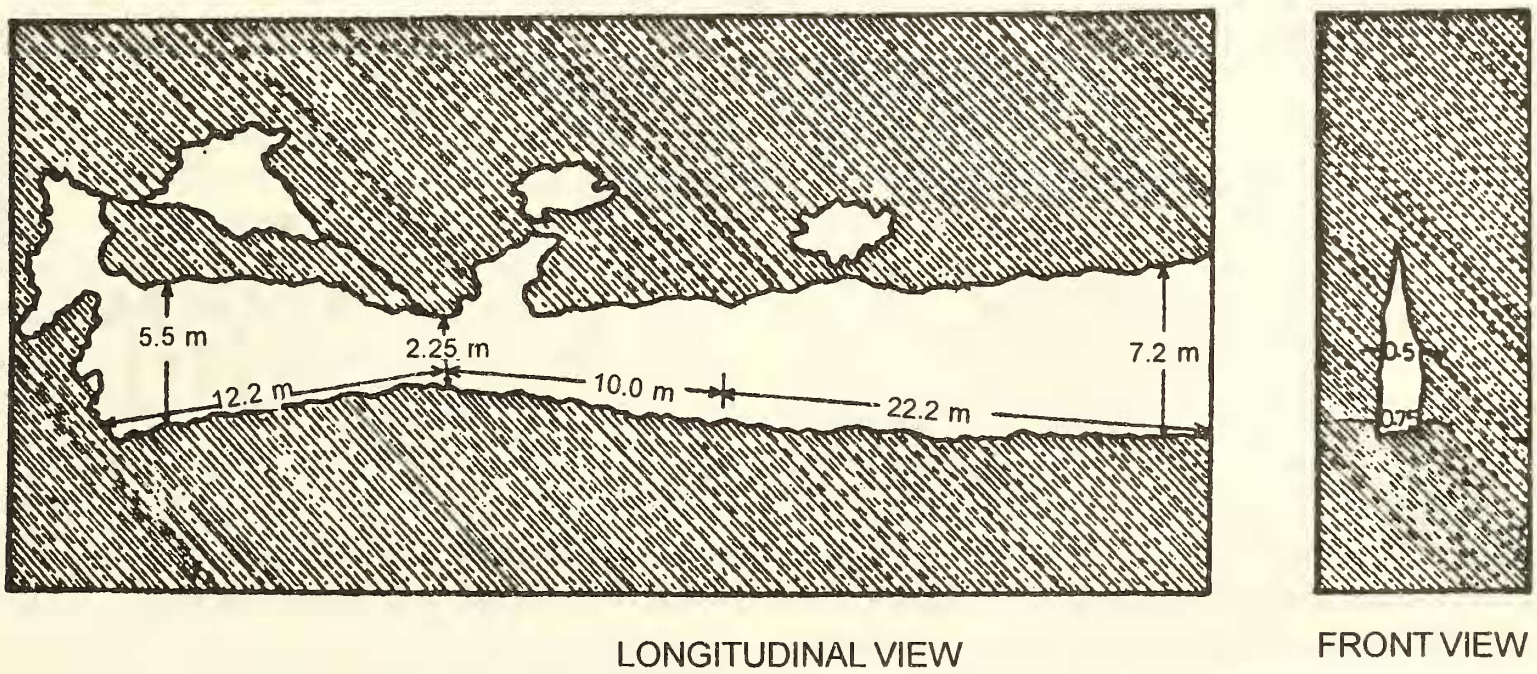
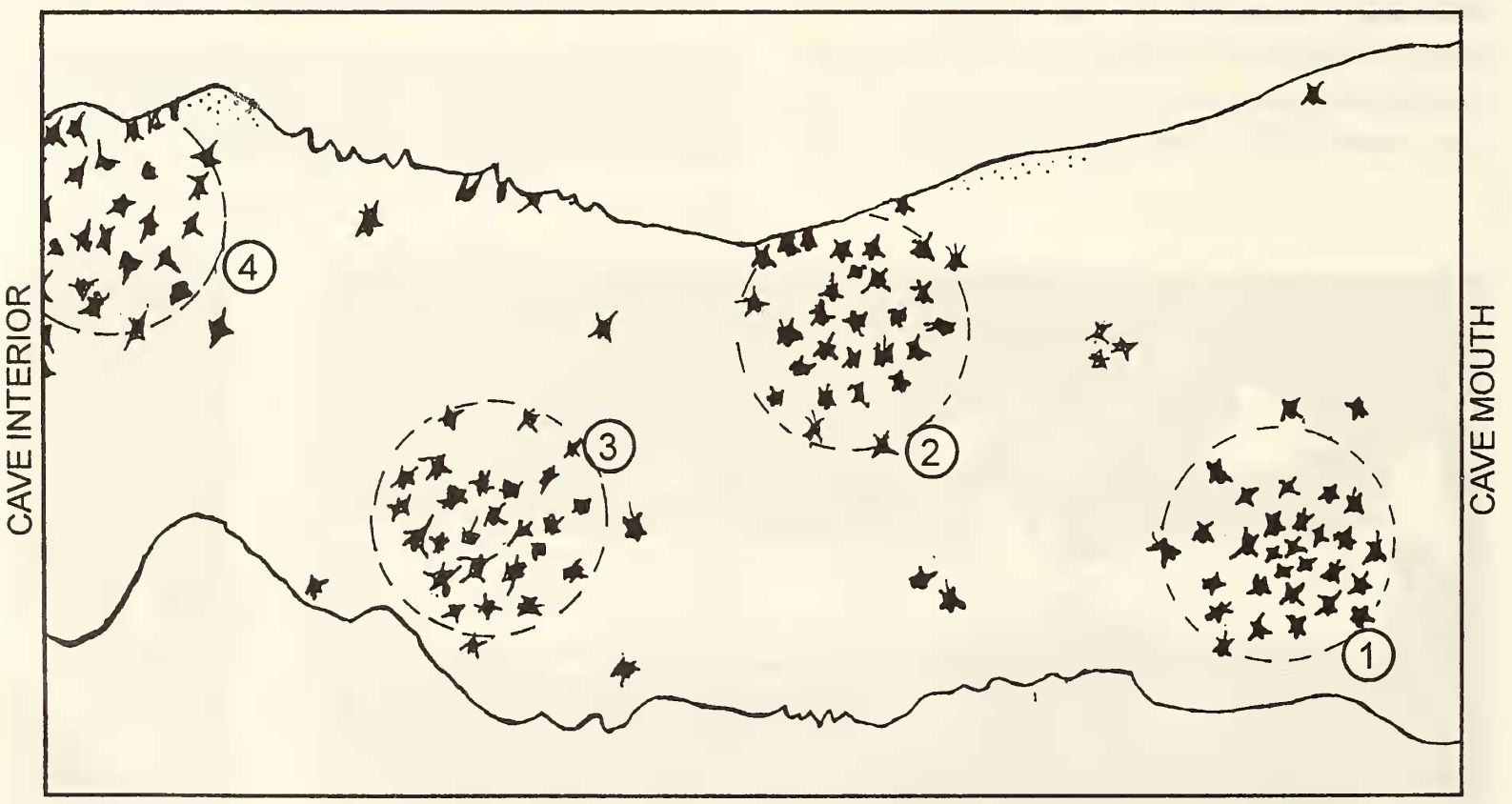


Fig. 9: Topology and dimensions of the cave inhabited by the colony of *Rhinopoma hardwickei*

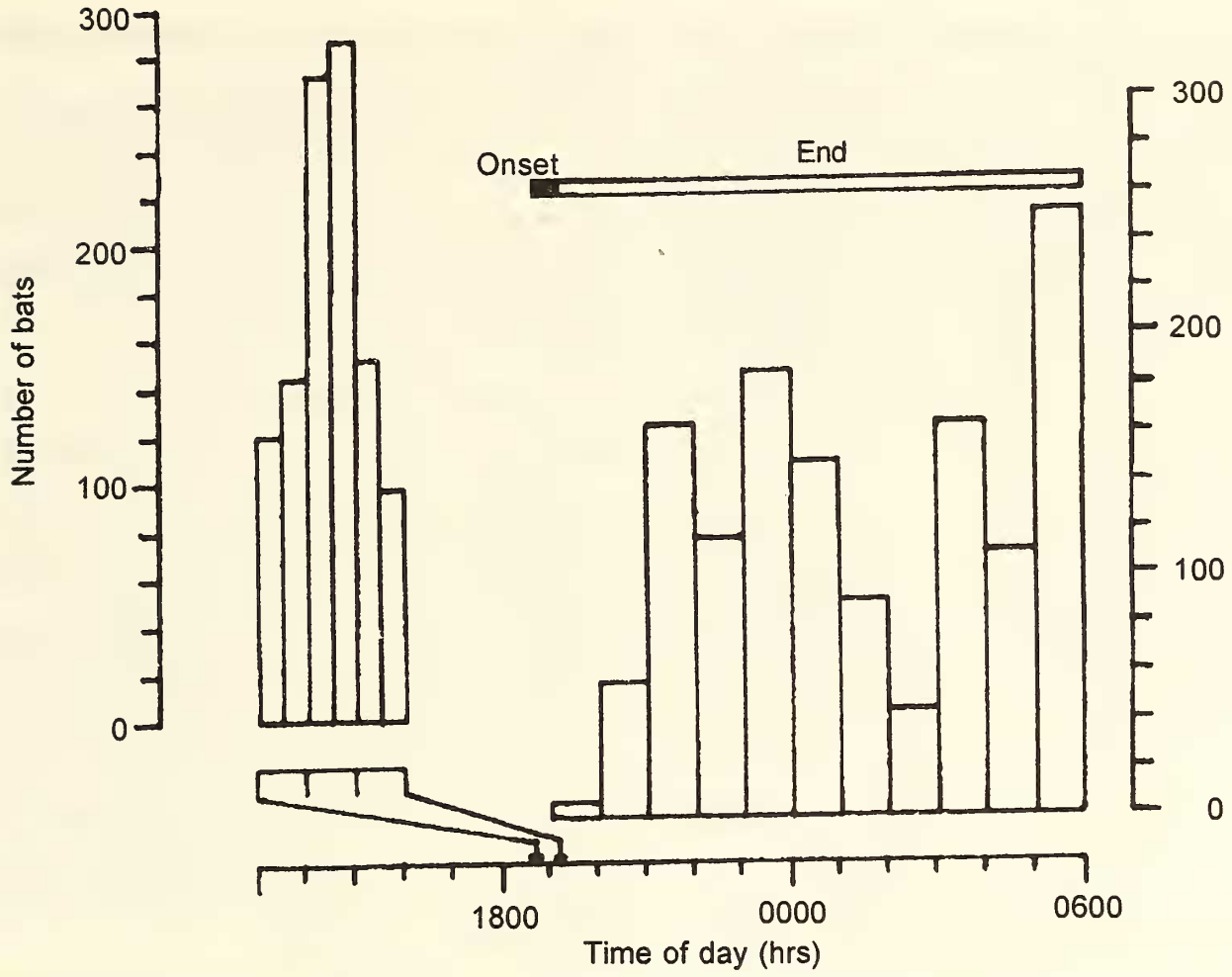
The *Rhinopoma* colony was also the biggest in terms of numbers. Prior to exodus flight, the members of the colony indulged in intense audible and shrill vocalisation which was literally amplified at the cave mouth. Fig. 11 summarises patterns of onset of colony activity accompanying sunset and return of the bats after foraging (Usman *et al.* 1990). The exodus flight is impressive, like a cloudburst, with the members scattering to fly to their foraging sites. Emergence of the colony kept pace with the seasonally varying time of sunset and the ambient light at the cave mouth, which varied between 1.0 lux during shorter days to 60 lux during the longer days of summer.

One striking feature, which is common to the nightly emergence of the colonies of *T. melanopogon, H. speoris* and *R. hardwickei,* is that the members of the colonies pour out synchronously. However, the return flight is spread over the night and not predictable. Based on such observations, we postulated (Chandrashekaran *et al.* 1983) that the arousal and onset of activity in these animals might be under the control of the circadian clock, whereas the end of activity may be determined by external environmental factors such as wind direction and speed, heavy precipitation and satiation. The most spectacular 'emergence by coup' of bats I had witnessed was on January 12, 2002, in Thailand. I was driven from Bangkok, to a place called Phu Phaman in Khon Kean province, some 450 km northeast, to watch a colony of bats emerge for their evening foraging. My informants themselves had not seen the phenomenon and therefore could not prepare me for the sight awaiting us. We arrived at the impressive cave site situated in a massive rocky hill with a yawning mouth *c.* 50 m high and 30 m across. There were eight tourist buses and hundreds of tourists who were all gazing at the cave. At 1745 hrs, the crowd gasped and we saw a thick black cloud ooze out of the cave and stream along the left flank of the rock at a height of 150 to 170 m. The bottom ledge of the cave mouth was at an elevation of *c.* 80 to 100 m.



Encircled numbers indicate positions of roosting at given time: 1. 0600-0900 hrs, 2. 0900-1200 hrs, 3. 1200-1500 hrs, 4. 1500-1800 hrs

Fig. 10: Rough illustration of daytime movements of a cluster of *Rhinopoma* bats



Outward flight of colony lasted only 26 minutes (1846 to 1912 hrs) on the evening of counting but return lasted virtually the rest of the night.

Fig. 11: Pattern of 'onset' and 'end' of the nightly foraging activity of the colony of *R. hardwickei* (After Chandrashekaran *et al.* 1983)

They looked, at that distance, like a swarm of bees, but too numerous to count or even guess the numbers. The sun had not set and several kites were gliding aloft. The outflow of thousands upon thousands of the bats continued steadily and lasted seventeen minutes when I saw the last of the millions of bats fly out at a great height, but this time headed in our direction. We were fortunate that a juvenile bat, possibly on his first evening out, fell to the ground close to me. I picked it up, examined it and placed it on a nearby rock. Given its resemblance to *Tadarida aegyptiaca* in Madurai, I presumed that the Thailand bat was *Tadarida brasiliensis*. The fur was dark grey, the bat was wrinkle-lipped, and had a snout like a mastiff. If the species was indeed *Tadarida brasiliensis*, then they were all flying out at great speed of 27 m/s, the fastest bat flight known (Neuweiler 2000). The temperature was 26 °C and darkness descended very soon. Dr. Manjunatha Rao, who took me to the Phu Phaman caves, writes that there are several other caves nearby. I was thrilled to see lovely, stylised statues in bronze, of the locally available bat species, inscribed with the Latin names.

Social synchronisation of circadian rhythms in *Hipposideros speoris*: An interesting feature that we noticed in the exodus flight of the *H. speoris* colony was that bats inhabiting the innermost recesses of the cave, mostly females and subadult males, were the earliest to fly out. A group of Dutch scientists (Voute *et al.* 1974) had noticed a similar phenomenon in the evening exodus flight of a colony of *Myotis dasyncheme.* A major question was: how do bats inhabiting the depths of our natural cave of perpetual darkness, invariant temperature and relative humidity — an environment virtually devoid of time cues — know the time of sunset in Madurai?

We made the first observations inside the cave (Marimuthu *et al.* 1978) with the help of infrared noctovision binoculars. The individuals of the colony were spaced out and hanging by their hind feet from the ceiling. If we approached them, they turned their heads in all directions with quivering ears and flew away if we went too close. But when Marimuthu and I sat still in the afternoon hours, the bats became still and the colony appeared to be in a state of deep rest (sleep?) until *c.* 1700 hrs. Soon after, the bats appeared to show signs of arousal and individual bats stretched their wings, began preening themselves, yawned and began flying about, one by one. Deep in this cave, where we made our observations, the gurgle of an unseen stream of water could be heard. Happenings subsequent to 'arousal' of the colony, such as bats flying to the light sampling chamber, and eventual exodus flight of the members of the colony soon after sunset have been described under 'Activity/ roosting patterns of a colony of *Hipposideros speoris*.'

The next question to be tackled was whether each bat had to 'see' for itself the darkening sky outside. If some bats did not come to the cave mouth to sample light, would they still know that the sun has set? Do the volunteer bats relay the information to bats deep inside the cave? We performed the first experiment in which we kept three male bats captive at a depth of *c.* 40 m in flight activity cages (described earlier) for an extended period of 50 days and the bouts of their flight and rest were continuously recorded on the charts of hand-wound thermohygrograph drums described earlier. It soon became apparent that the captive bats began their flight activity at the precise time at which the free-flying conspecifics began their evening exodus flight. The actogram describing the flight activity/rest patterns of the three captive male bats for 40 days in one case, and 50 days in the other two cases, is presented in Fig. 12 (Marimuthu *et al.* 1981). The 24-hour activity/rest strips were pasted on bristol board one below the other chronologically. Activity bouts are indicated by the vertical patches and the horizontal traces indicate rest.

The captive bats were less active when the cave emptied out, but they responded to stray returning bats and to the flock of bats returning in the small hours of the morning. Our excitement was great, for we had confirmed that the free flying bats were telling captive bats the time. Our first communication (Marimuthu *et al.* 1978) was a very short one of less than 400 words based on activity/ rest patterns of one captive bat recorded for a mere eleven days inside the cave. Confirmatory evidence of social synchronisation (that is the scientific term) of the circadian rhythms in *H. speoris* came with a later paper (Marimuthu *et al.* 1981). We had also stated that it was not clear to us how the phenomenon took place and suggested involvement of: 1) pheromones, 2) wing flapping noise generated when conspecifics flew out, and 3) acoustic transmission of message.

Even though we were reasonably sure that there was social information of sunset and time of day, we wanted to demonstrate the opposite situation also, i.e. a solitary bat in a solitary cave without 'social informers' cannot synchronise its circadian rhythm to the 24-hour periodicity of bat colony activity. A practical problem was finding a cave good enough to be habitable for bats but still not colonised. When, finally, we did find a solitary cave without hipposiderid bats, we performed an experiment by placing a solitary male *H. speoris* in a flight activity cage and recorded its flight activity/rest patterns inside the cave. The solitary bat was indeed helpless in the strict 24-hour periodicity of the onset and end of its activity, as is shown in Fig. 13. The circadian activity rhythm in the flight activity free-ran with a period < 24 hours in the continuous darkness of the cave (Marimuthu *et al.* 1981). The bat began its nightly flight *c.* 20 mins earlier each *subjective* evening. We terminated our experiment with a touch of bravura. After 50 days in captivity and free-run of its circadian rhythm, our bat began its

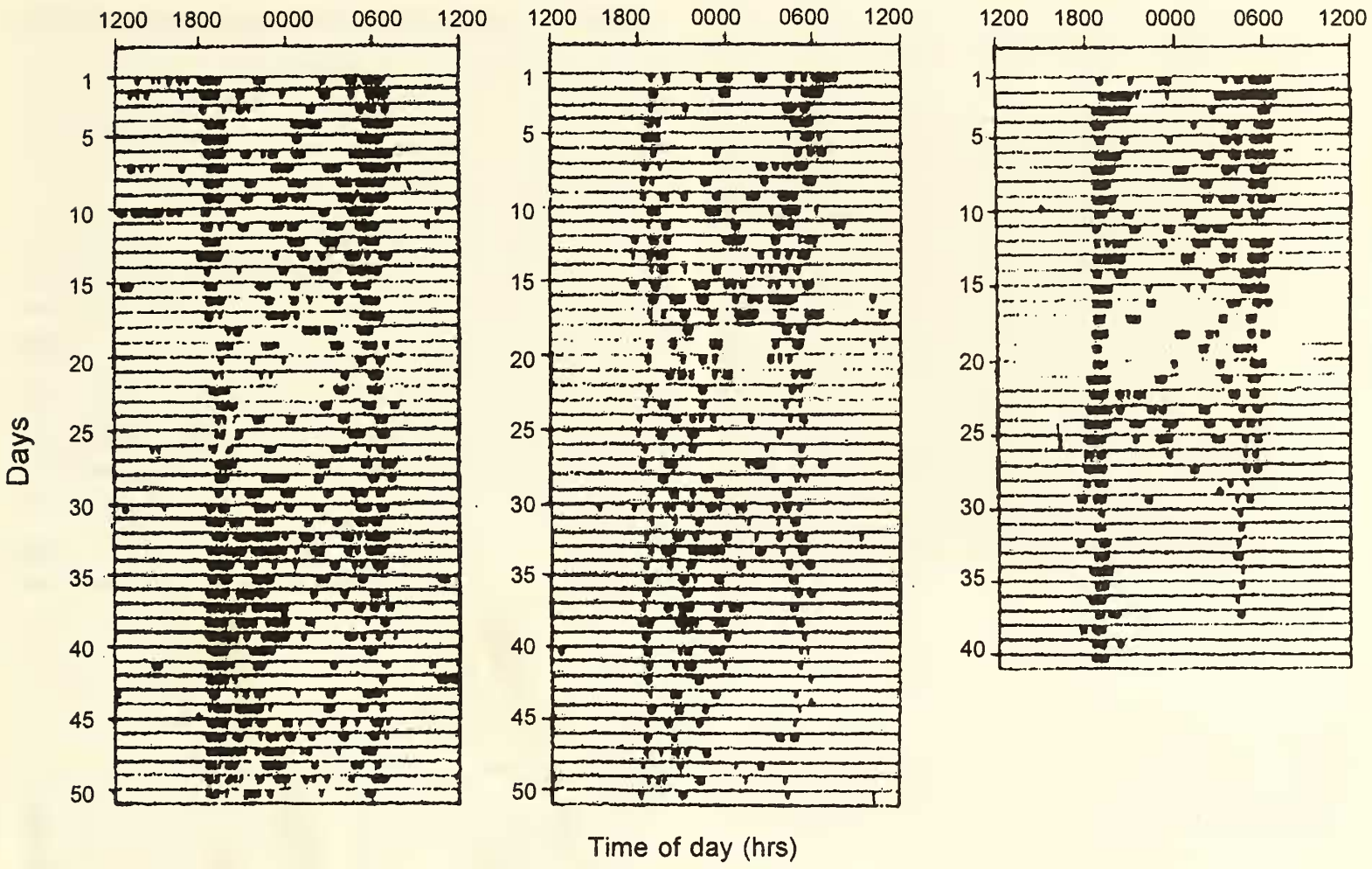


Fig. 12: Actogram showing flight activity patterns of three captive male *Hipposideros speoris* bats (After Marimuthu *et al.* 1981)

nightly activity just when other free flying bats were *returning* to the roost in the early hours of the civil morning.

Please note that, as shown in Fig. 13, the bat started its nightly activity close to 1900 hrs which is near civil sunset time. On a daytime inspection on day 10, it turned out that the cave was not impervious to bird calls (crows and mynas at a nearby watering hole), at night resident crickets stridulated. It looked as if the solitary bat was taking time cues from these acoustic inputs, but I was sceptical of such interspecific acoustic entrainment and we continued the recordings. To our surprise and excitement, the circadian rhythm slipped into a state of free-run (as explained above) from day 11 onwards (as seen in Fig. 13). The obvious interpretation is that birds and crickets cannot entrain the circadian rhythm of this captive bat. These observations led us to another major question. Do these bats need to be told the time by other bats of the same species? In other words, is social synchronisation in *Hipposideros speoris* species-specific?

There have been interesting reports of species-specific entrainment of perch hopping rhythmicity of the common sparrow *Passer domesticus.* Male courtship vocalisations were played back to female sparrows held in continuous dim light for four and half hours in a 24-hour cycle, and the perch hopping, free-running circadian rhythmicity entrained to song/silence cycles (Gwinner 1966). Similar results came in for two other species of birds the same year and these results generated much excitement for their ecological and behavioural implications. However, a year later it was found (Lohmann and Enright 1967), rather unromantically, that cycles of mechanical noise administered by a loud buzzer

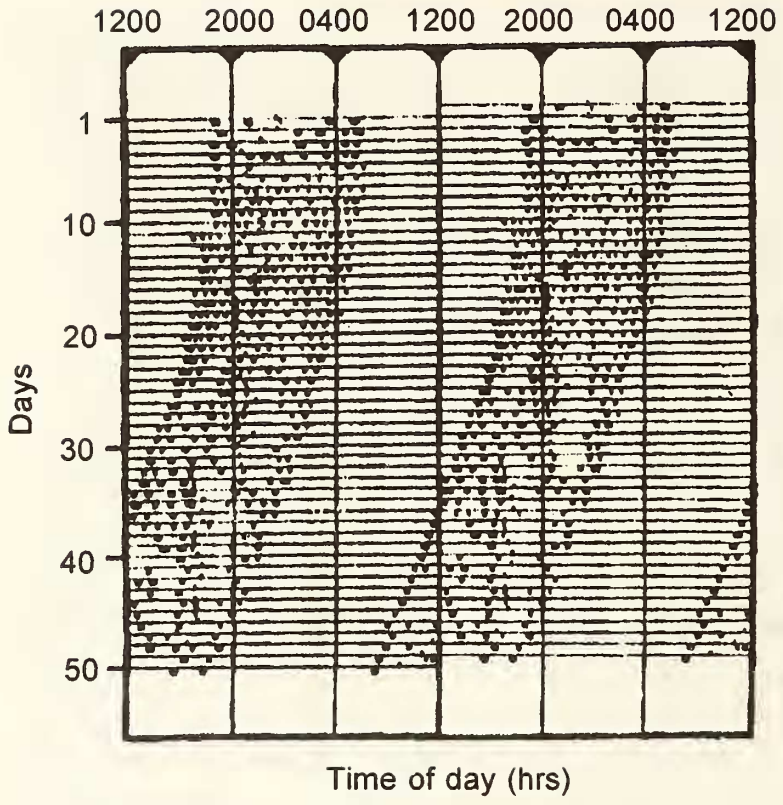
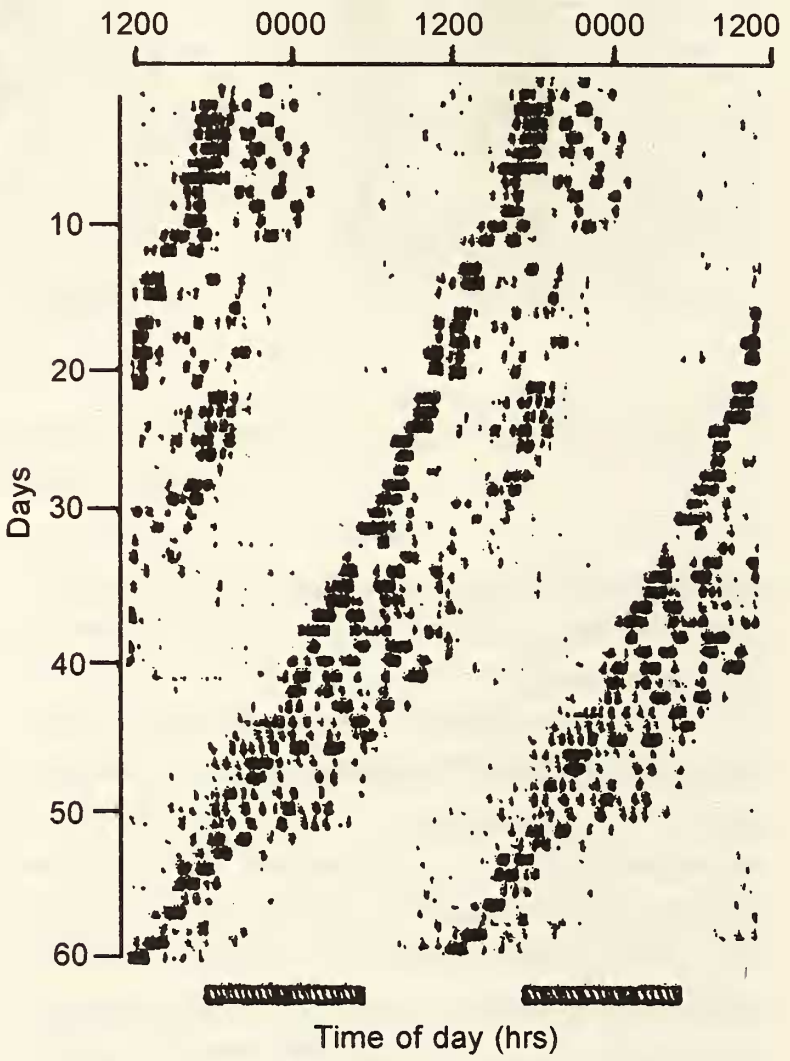


Fig. 13: A double plot of activity/rest patterns of a solitary male *Hipposideros speoris* bat recorded in an empty cave without any conspecifics over a period of 50 days (After Marimuthu *et al.* 1981)

for a few hours in a 24-hour cycle, also entrained the activity rhythms of three species of passerine birds. This is a demonstration of the phenomenon of non-species-specific entrainment of circadian rhythms at its best.

To return to bats, in order to investigate the possibility of species-specificity in social synchronisation of circadian rhythms in bats, we performed an ingenious experiment. We introduced a rank outsider bat, an alien species, a male *Taphozous kachhensis* into the *Hipposideros speoris* cave in the Jain Hills, and recorded its flight/rest pattern while captive. The circadian rhythm of flight/rest activity of the alien could not be socially (or otherwise) entrained by the 550-600 hipposiderid residents (Marimuthu and Chandrashekaran 1983a). The circadian rhythm of the emballonurid *T. kacchensis* impressively free-runs as shown in Fig. 14. We interpreted the results as indicating a kind of communication gap between the hipposiderids and the alien emballonurid. We can back up claims from the results of neurophysiological experiments in which we placed electrodes in the lower colliculus of a *T. kachhensis* bat in the operation theatre and played back the colony vocalisations (including ultrasonic acoustics) of *H. speoris* (using a homemade Lennartz tape recorder of 2-200 kHz range). The emballonurid bat (under mild nembutal narcosis) showed no spike (action potential) responses. The message was not even being heard. These results strongly suggest that social synchronisation of circadian rhythms in microchiropteran bats may indeed be species-



Hatched area at bottom describes hours of exodus activity during early night and returning of the resident, free-flying *Hipposideros speoris* bats.

Fig. 14: Double-plotted actogram illustrating the free-running of the circadian rhythm in the flight activity pattern of an emballonurid bat *Taphozous kachhensis* confined to a hipposiderid (*H. speoris*) cave for 60 days (After Marimuthu and Chandrashekaran 1983a)

specific. The interesting field observation is that, in some places, *H. speoris* and *T. kachhensis* are known to share roosting sites (pers. observ., also Brosset 1962).

We have established for the first time that: 1) the circadian rhythm of a captive bat held in isolation in perpetual darkness free-runs, and 2) in the presence of free flying conspecifics which undertake foraging flights out of the cave and back, the circadian rhythms of captive bats entrain to the 24-hour periodicity of flight/rest of the colony. Thanks to the light/darkness of the natural environment (ubiquitous entraining agents) there are no free-running rhythms out there in nature, except in deep-sea organisms and those living in caves (Koilraj *et al.* 2000). Circadian rhythms are also known to free-run in organisms in the Arctic winter (of perpetual darkness) and summer (of continuous light) (Bünning 1973). We were curious to know how bats dwelling in the darkness of caves and foraging in further darkness of nights would respond to exposure to continuous light — an admittedly artificial condition that these tropical bats never face. Artificial light was created with car batteries and an incandescent bulb inside the *Hipposideros speoris* cave, and the flight activity/rest patterns of three male captive bats, in activity cages placed in the vicinity of the light bulb, were measured. The ambient light intensity at the level of the cages was between 5 to 15 lux. It can be seen from Fig. 15 that the circadian rhythms in the activity/rest patterns in all three bats free-ran (Marimuthu and Chandrashekaran 1983b) with a period > 24 hours. Continuous light lengthens period and perpetual darkness shortens it, in these dark active animals, effects that have been codified in 'Aschoff's Rule' (Aschoff 1960, Pittendrigh 1960). A careful examination of Fig. 15 will reveal two 'conflicting' components. All three bats do stir about briefly during the colony's exodus flight, but lapse into sleep and begin and end activity according to their endogenous circadian free-running schedule with a period >24 hours. The brief arousal during colony exodus coinciding with sunset is called a positive masking effect (Aschoff *et al.* 1982), and the free-run, the true expression of the circadian clock, which is apparently uncoupled from the 24-hour social synchronising inputs, by the artificially created continuous light. In spite of close to ten years of working on the social synchronisation of circadian rhythms in *H. speoris* we are still, quite literally, in

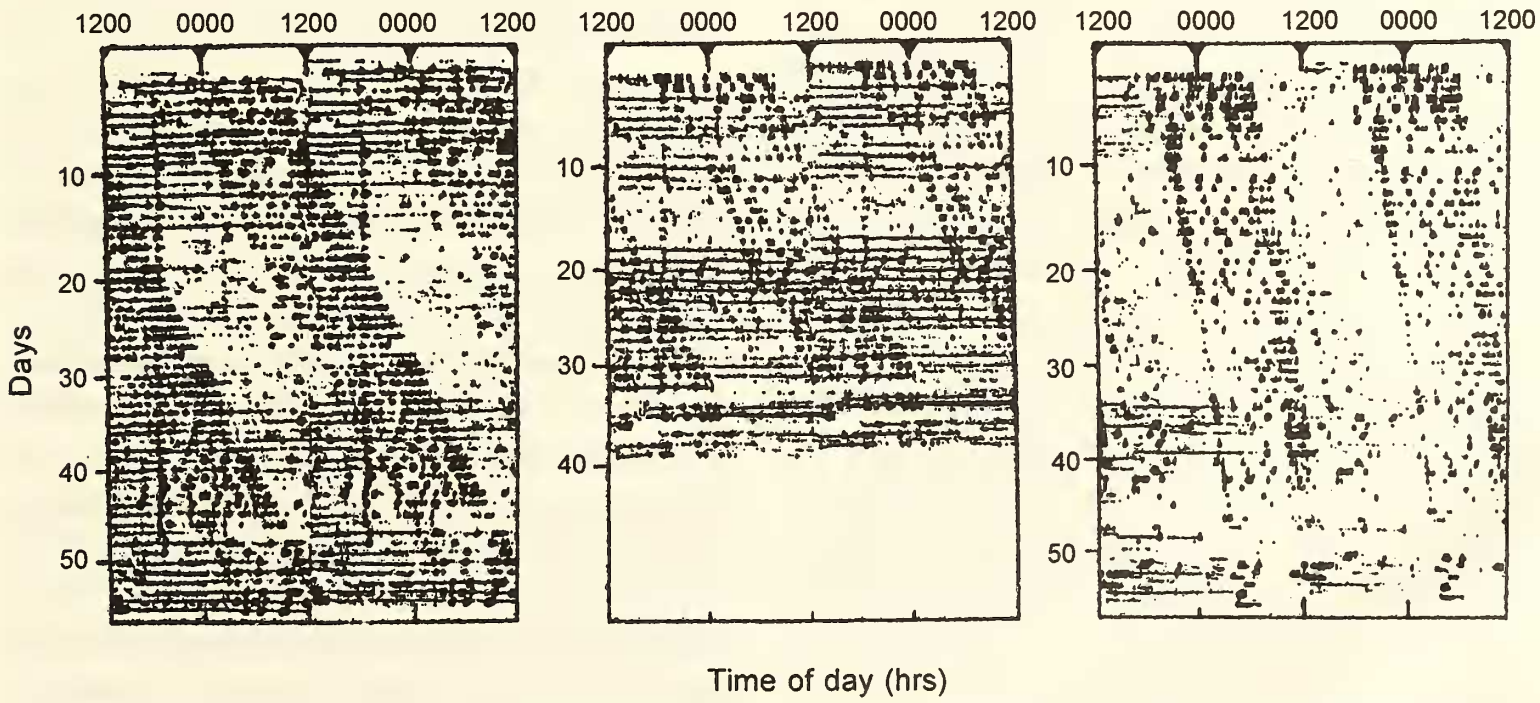


Fig. 15: The flight activity patterns of three captive male *H. speoris* bats for durations of 55 days (a and c) and 39 days (b), registered in LL of 10 to 20 lux (After Marimuthu and Chandrashekaran 1983b)

the dark about the exact nature of the social cues (ultrasonic acoustics? pheromones? wing-flapping noise of free flying bats?) behind this kind of entrainment.

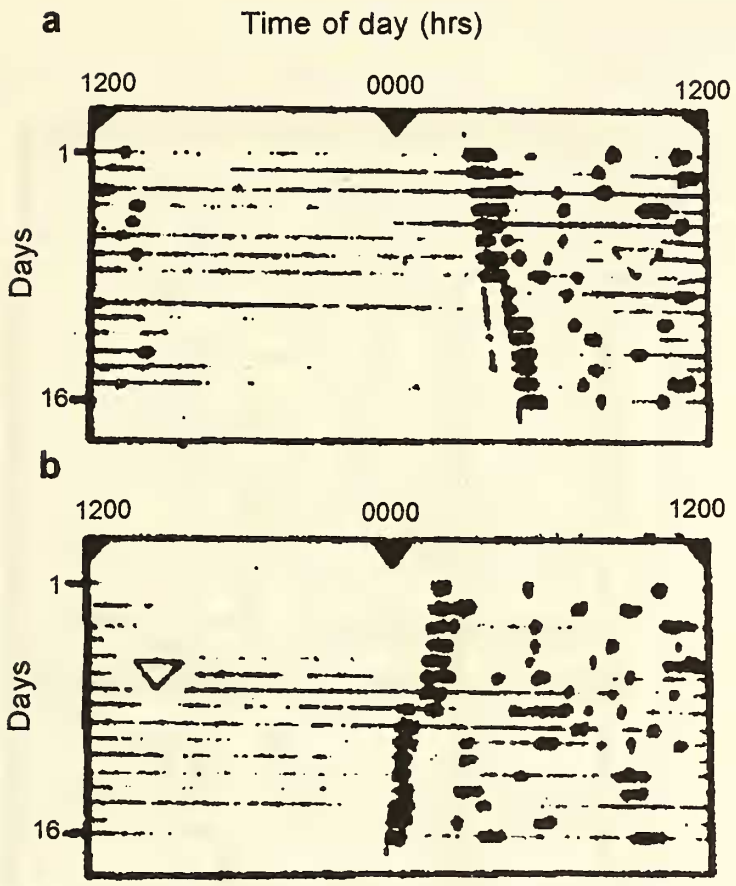
One of the earliest reports to impute social synchronisation among conspecifics was for mice of the genus *Peromyscus* (Halberg *et al.* 1954). Similar effects have been subsequently claimed for blinded mice, male chevrotain antelopes, wolf-coyote hybrids, beaver colonies of *Castor canadensis*, macaques and sexual cyclicity of female mammals (for an early review, see Chandrashekaran 1982). Social synchronisation of circadian rhythms deserves to be better studied, preferably using social insects such as honeybees and ants (Frisch and Aschoff 1987).

A daylight PRC for the circadian rhythm of *Hipposideros speoris*

The 'phase response curve' (PRC) is a plot of the responses of a circadian rhythm in terms of phase shifts to perturbations (of light, temperature, and chemicals) as a function of phase. A vast body of scientific literature has accumulated on this subject. A PRC informs the state of sensitivity of the basic oscillator (biological clock) at any given phase to the zeitberger stimuli (perturbations). Such information cannot be had, for instance, when we record discrete events such as locomotion and rest, which start and end abruptly. There is no clue to the state of the clock during hours of rest when nothing happens outwardly. Further, all external events, both observable and measurable, may be of the nature of the 'hands of the clock'. Pittendrigh (1960) stated that the *Drosophila* PRC reflected the time course and waveform of the basic oscillator. All experimental studies to construct PRCs have been made with fluorescent and incandescent light (Chandrashekaran 1998). We therefore constructed a daylight PRC for the circadian rhythm of the cave dwelling bat *Hipposideros speoris,* employing brief pulses of daylight for perturbations and performing the arduous experiments inside a natural cave. The dimensions of this cave were less cramped (12 x 8 x 2.5 m), with uneven walls, ceiling and floor. The 5 original inhabitant bats (*H. speoris*) were evicted, and the cave was fitted with blinds and lightproof doors. Temperature was constant at 28 ±1°C and relative humidity of 85 ±5% prevailed. Employing methods described earlier, the flight activity/rest patterns were recorded on Lambrecht-KG-Göttingen thermohygrograph drums. The bats were brought to the cave mouth (close to the hinged door) at different phases of the circadian rhythm and exposed to diffuse daylight of *c.* 1000 lux for 15 minutes. Fig. 16 illustrates a typical delay phase shift and a typical advance phase shift of the flight activity, and Fig. 17 illustrates the PRC obtained on many bats. The daylight PRC we obtained resembles those made for other organisms using fluorescent and incandescent light (Joshi and Chandrashekaran 1983).

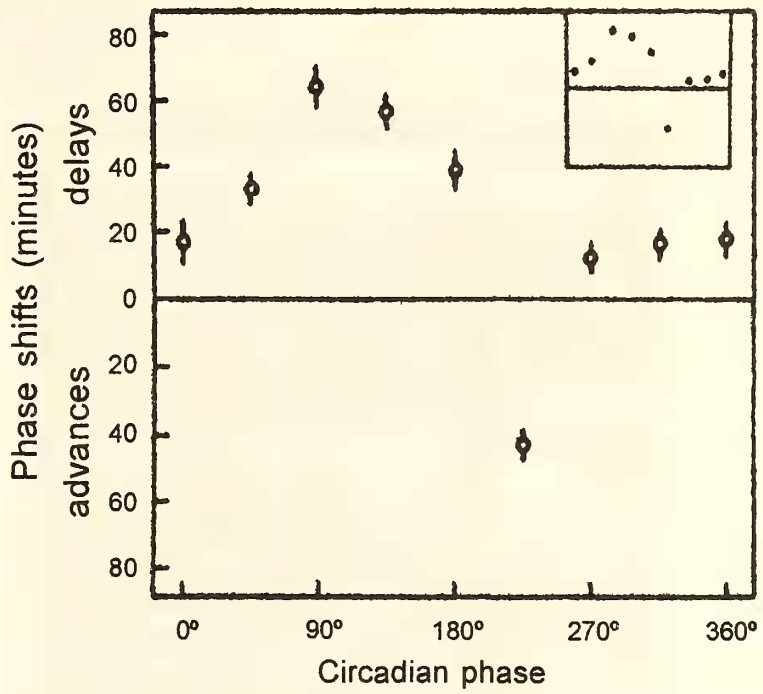
Daylight dimmer than starlight entrains *Hipposideros* rhythm: I report an accidental finding which we later investigated at some length. This happened in the cave inside which Dilip Joshi had worked out the PRC. Another student, S. Rajan brought in a chart depicting the flight activity of a solitary male *H. speoris* for a period of 47 days under absolute darkness, constant temperature and relative humidity. The activity started at around 1900 hrs, evening after evening, and stopped a little before sunrise. The calculated period length was exactly 24 hours, unheard of in the literature on circadian rhythms. This made me write an eccentric paper, 'An unusual circadian rhythm with a precise 24-hour period' (Chandrashekaran 1981). I philosophised "The law of parsimony dictates that we consider our 24-hour bat as an *isolated* instance of a circadian system quite accidentally possessing a very uncircadian circadian rhythm!"

Then Dilip Joshi brought in 4 or 5 other cases of bats with precise 24-hour periods. To make a long story short, light was apparently leaking in. Careful scrutiny revealed a crack in the uneven ceiling of the cave through which very



a. Illustrates a delay phase shift of 63 minutes at 90° phase of light exposure.
b. Illustrates an advance phase shift of 42 minutes at 225° phase of light exposure.
∇ = light exposure

Fig. 16: Phase shifts caused in the flight activity rhythm of two male *Hipposideros speoris* bats by 15 mins exposure of the animals held in DD to diffuse daylight of *c*. 1000 lux (After Joshi and Chandrashekaran 1983)



Open circles = Mean; Vertical lines = SD. n = 4 or 5

Fig. 17: PRC obtained for the circadian rhythm in the flight activity of *Hipposideros speoris* in DD inside a cave on several bats, and for a solitary bat (PRC in inset), over a protracted period of 156 days with 15 minutes daylight of *c*. 1000 lux (After Joshi and Chandrashekaran 1983)

dim light in the range of 0.0001 to 0.0006 lux streamed in. Due to the inclination of the crack the light came in for just *c*. 90 to 100 minutes during midday hours. Light intensity was measured (with a UDT optometer on the log-scale, i.e. time x intensity) where it shone the brightest on the floor of the cave.

Two experiments were performed with 4 and 3 bats. All these bats entrained. Fig. 18 shows the pattern of entrainment of two bats used in the first experiment over periods of 39 days (Fig. 18a) and 35 days (Fig. 18b) respectively, in response to very dim light of 0.0001 to 0.0006 lux illumining the bats for *c*. 1.5 hours. Onset of activity coincided with the local sunset time. Results of the second experiment confirm that the entrainment was indeed effected only by the dim light. Fig. 19 shows entrainment of the flight activity in 2 bats during the first 18 days. Then the light leak was plugged. In one bat the free-run of the rhythm set in immediately (Fig. 19a) with a period < 24 hours, and the other bat continued in the entrained rhythm for 2 weeks before its rhythm free-ran with a period >24 hours (Fig. 19b) (Joshi and Chandrashekaran 1982). An interesting feature of entrainment in this case was that even though the bats experienced exposure to the dim light at midday, the onset of activity coincided with local sunset time 6 to 7 hours later. Obviously, the light pulse in addition to entraining also influences the phase angle. In other words, the bats recognised the dim light to be midday light. We had speculated that this phenomenon might have an adaptive value.

The lowest intensity of light reported in literature as entraining a circadian rhythm (in the

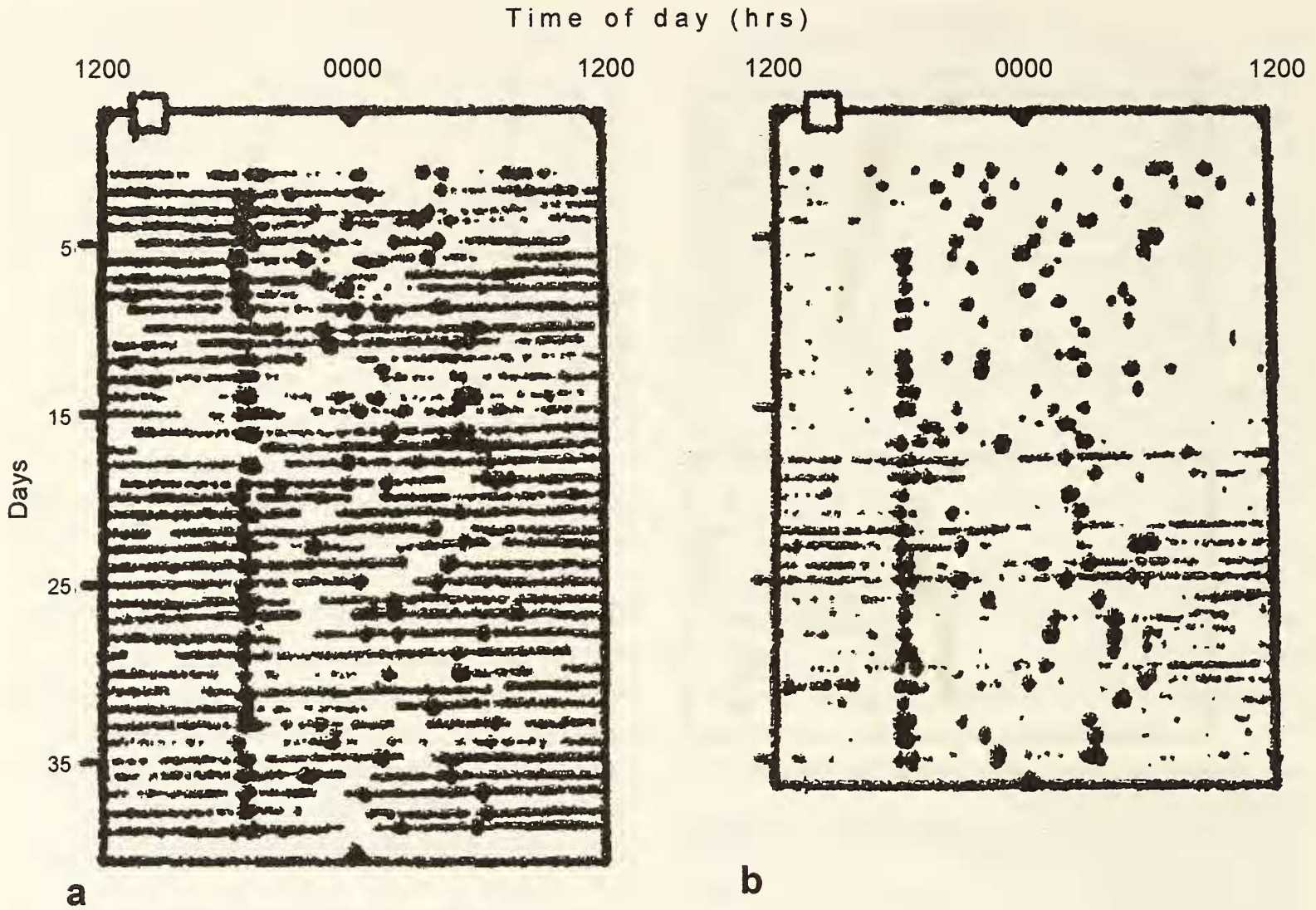


Fig. 18: Entrainment of the flight activity rhythms of two male *Hipposideros speoris* bats inside a natural cave for 39 days (a) and 35 days (b) in response to *c.* 90 mins of dim light of 0.0001 to 0.0006 lux streaming in at midday hours (box at top) (After Joshi and Chandrashekaran 1982)

sensitivity of the median eye of the scorpion *Androctonus australis* L.) is 0.00025 lux shone continuously for 16 hours (Fleissner 1977). It must be pointed out that the actual light intensity at the level of the flight activity cages, positioned approximately 2 to 3 m away from the site of light measurement, was beyond the sensitivity of our optometer. The intensities of daylight that entered the cave were about 5% to 30% of starlight intensity. These are to date the lowest intensities of light implicated in entrainment of circadian rhythms. We have also constructed PRCs for ultra-short light pulses of 0.0625 milliseconds, for the circadian rhythm in the flight activity of *Hipposideros speoris*, which are the shortest light pulses in literature, demonstrated to shift phase (Joshi and Chandrashekaran 1985a).

Spectral sensitivity of the photoreceptors in *H. speoris*: Do the bats have colour vision? We performed a series of experiments to study the spectral sensitivity of the photoreceptors responsible for phase shifting the circadian rhythm of flight activity in the bat *H. speoris*. In nature, these bats exist in a strange paradoxical light-darkness regimen experiencing absolute darkness during the daytime inside natural caves where they roost, and some amount of light (starlight, moonlight) during the night when they forage in the open. They are thus exposed to skeletal pulses of dim twilight of 4-40 lux in intensity, during dawn and again during dusk on the same day, that constitute the major phase resetting stimuli responsible for entrainment by natural light.

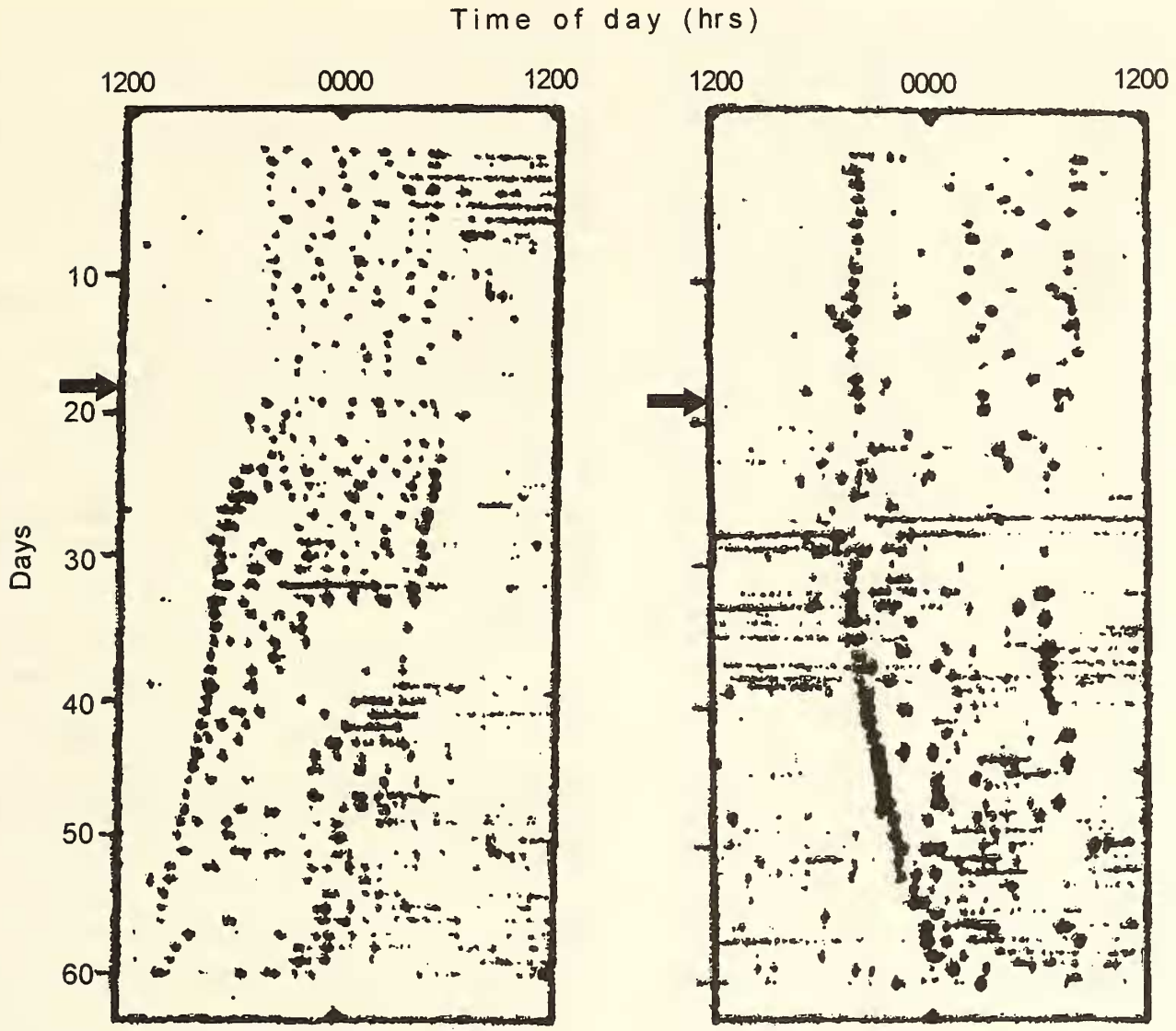


Fig. 19: Pattern of flight activity rhythms of two captive male *Hipposideros speoris* bats inside the DD of a cave for 60 days. Entrainment ensues for 18 days (a) and 33 days (b) in response to very dim light streaming through a crack in the ceiling. The leak was fixed on day 18 (indicated by arrow)
(After Joshi and Chandrashekaran 1982)

We have monitored the phase shifts evoked when the circadian rhythms, free-running in constant darkness, were exposed to 15 minute and 2.77 hour pulses of monochromatic light (100 $\mu W/cm^2$) at various phases. Fig. 20 illustrates the flight activity record of a bat in DD for 275 days, exposed at various phases to monochromatic light pulses. The marathon experiment lasted 275 days and the actogram shows long lasting changes in period that followed some phase shifts. For these experiments, four phases were chosen to investigate the wavelength dependent phase shifts, and we reported that light pulses of 430 and 520 nm unequivocally delay (at CT 18 hrs) and advance (at CT 4 hrs) the phases, respectively. It was postulated that there might exist *two* classes of photoreceptors in the retina of *H. speoris*. The S photoreceptors (short wavelength sensitive) having a maximum sensitivity at 430 nm and the M photoreceptors (middle wavelength sensitive) having maximum sensitivity at 520 nm, that mediate delay and advance phase shifts (Joshi and Chandrashekaran 1985b). This is illustrated in Fig. 21. The data presented in the figure was derived from 156 phase responses for 36 bats; for each point at least four measurements were taken.

Prey capture by the false Indian vampire bat: *Megaderma lyra* (Body weight 31-35 g, best hearing frequencies 11-65 kHz)

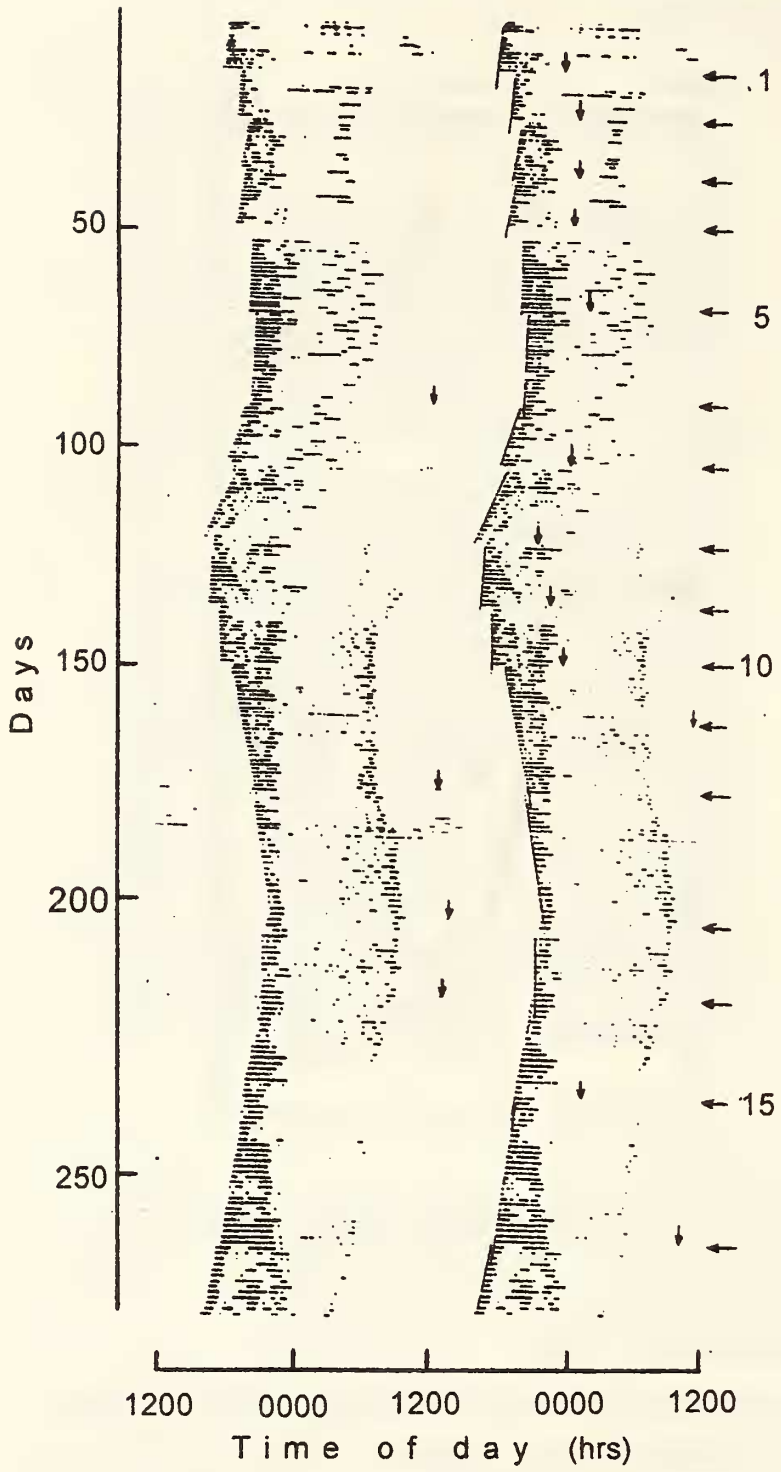
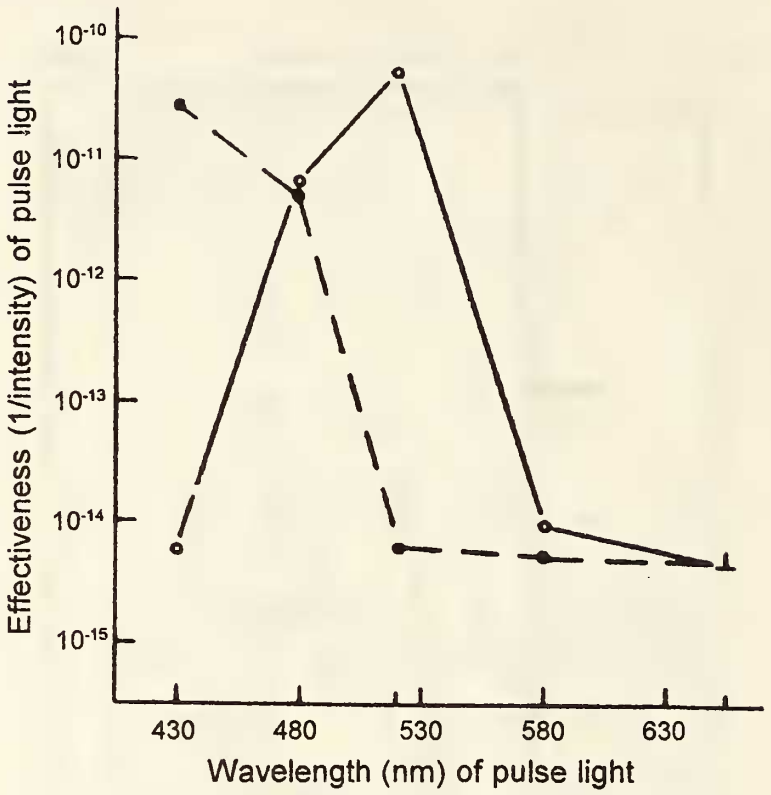


Fig. 20: Flight activity record of a male *H. speoris* bat held in DD exposed to monochromatic light pulses of higher energies of 100 μW/cm² for durations of 2.77 hours given at different phases (pulses 2 to 16). Horizontal arrows to the right indicate the phases at which the light pulses were given (After Joshi and Chandrashekaran 1985b)



Advance phase shifts (CT 4 hrs) = solid line, maximum at 520 nm. Delay phase shifts (CT 18 hrs) = broken line, maximum at 430 nm.

Fig. 21: The spectral sensitivity curves obtained with 15 minute monochromatic light pulses that evoked approximately 50% of the maximal advance and delay phase shifts evoked by white light pulses at CT 4 hrs and CT 18 hrs phases, respectively (After Joshi and Chandrashekaran 1985b)

The biggest colony of the false Indian vampire bat *Megaderma lyra* lived in a very well camouflaged cave, on the southern slope of Nagamalai Ridge to the west of MKU, which was difficult for humans to approach. This bat is unique among Microchiroptera because its diet is eclectic, including small vertebrates, birds, reptiles and mammals. Our German colleagues maintain their colony of *M. lyra*, captured in and around Madurai, in Munich, offering each bat one live mouse a day. In our laboratory, we had at least twelve *M. lyra* at any given time, let loose in the outdoor bat enclosure with a well stocked frog pond (dimensions given under '*Taphozous kachhensis*'. These bats, which are the most ferocious when handled, did their own foraging, feeding on the frogs that jumped out to the edge of the pond, or in water. G. Marimuthu has performed elegant experiments and reported the unusual modes of prey capture in *M. lyra*, on land and in water (Link *et al.* 1986, Marimuthu and Neuweiler 1987).

On land: Six to ten bats were used in the experiment. The bats generally hung from the steel rafters of the outdoor enclosure, visible during night, and inside the darkened wooden enclosure, during day. These bats need 'personal' space but unlike *H. speoris*, *M. lyra* huddle when they are disturbed in their natural haunts or are feeling threatened (Chandrashekaran and Marimuthu 1987). Also unlike *H. speoris*, the *M. lyra* stirred out of the darkened wooden enclosure into broad sunlight and hung from the steel rafters of the enclosure. Marimuthu released medium sized frogs on to the sandy floor of the outdoor cage and made the interesting discovery that only jumping frogs attracted the attention of the bats. If the frogs sat still, the bats did not take any notice of them. The moment a frog jumped, the bats, in threes and fours, swooped down to catch it, but only one of them succeeded in getting hold of the frog by its scruff. The victorious bat stayed for 2-3 seconds on the ground and used its wings to properly position the frog in its jaws. Then it flew up and off, back to its roosting position, to ingest in the next 3-5 minutes the entire frog head first, leaving only the hind legs, in interesting contrast to the tastes of humans in frog consumption (Marimuthu and Neuweiler 1987).

Marimuthu also demonstrated that dead frogs tied by twine and dragged over a sandy surface are promptly captured, but not dead frogs that are noiselessly dragged over a smooth glass pane over a thin sheet of water. It is clear that this gleaner was not detecting the motion of the prey but was listening to the "zic" noise of 10-15 kHz that jumping frogs made. This mode of prey capture by gleaners listening to the rustle of scampering prey on the ground, without resorting to echolocation, has been called 'passive acoustic localisation'.

In water: There are some species of bats that preferably hunt over rivers, lakes, and marine coastlines and take prey from the water surface. Such species are *Noctilio leporinus*, *N. labialis*, *Megaderma lyra* and *Myotis* spp. On field visits at night time, in areas rich in ponds and small waterbodies in south Madurai, one often noticed *Megaderma lyra* silently and swiftly fly past at a mere height of *c.* 1 m, obviously listening for scampering prey or jumping frogs. Some species of bats that hunt over ponds, rivers and lakes have enlarged feet with which they scoop up small fishes and arthropods from the water surface. An ideally smooth water surface would act as an acoustic mirror, making it difficult for echolocating bats to receive an echo. Water ripples and objects protruding from the surface create a kind of texture. Hunting *M. lyra* seem to detect the protruding snouts of stationary frogs in water, in this manner. Ultrasonic recordings indicate that the false vampire actively echolocate snouts of frogs, most of which remained strangely motionless (Marimuthu *et al.* 1995). While the bat hovers over the water, its flapping wings fan the air, which creates ripples in the water all around the snout of the frog below. *Megaderma lyra* presumably detects, using ultrasonics and echolocation, the outward progression of ripples *vis-à-vis* the motionless central protrusion of the snout of the frog. As soon as the hunting bat splashes into the water, the other frogs dive deeper into the pond and swim to safety.

The role of eyes in echolocating bats: The advantages of echolocation and the glamour surrounding the subject is such that extensive work has been carried out on this aspect (Neuweiler 1990). But surprisingly little is known about the precise use of the bats' eyes in vision and prey capture. A book devoted entirely to bats (Altringham 1996) makes only one reference (Bell 1985) to the function of vision in prey capture. It is common knowledge that hearing in microchiropteran bats is much more efficient than seeing. Morphologically, the auditory regions of the brain of insectivorous bats are disproportionately large compared to the optic regions. The auditory regions of the brain are specialised to receive, process, store and retrieve information about the environment on the basis of soft echoes.

We have not conducted specific experiments to investigate the role of the eyes of Madurai bats in landing or prey capture. The Madurai bats forage as efficiently on new moon nights as they do during a lunar eclipse (Usman *et al.* 1980). We, however, have evidence that *Hipposideros speoris* and *Rhinopoma hardwickei* did forage on insects in the pitch-black darkness of their caves. This often happened when there was heavy rainfall outside, coinciding with sunset and the bats could not fly out. Hordes of insects were driven into the caves by the gusts of wind. Link *et al.* (1986) have reported that *Rhinolophus rouxi*, *Hipposideros speoris* and *H. bicolor* approached and seized dead cockroaches held by forceps, when these were artificially vibrated. This indicates that any oscillating movements and not specific aspects of wing beating were the key stimulators for catching-behaviour in all three species. Once, Marimuthu was feeding bats held captive, in activity cages, 40 m deep into the Jain Hills cave. He was holding the live cockroaches with the aid of forceps. The elytra, wings, legs and innards of the insect had been removed. Even after this operation the cockroach usually wriggled between the tips of the forceps. On one occasion, a free flying *H. speoris* wrenched a wriggling cockroach off the forceps. On scanning the ceiling of the cave with a torch emitting 'safe' light of >630 nm, a male bat was found hanging from the ceiling, chewing the cockroach. This prey capture in absolute darkness was obviously accomplished solely by means of echolocation, in which *H. speoris* employs CF/FM signals of 5-10 milliseconds of pure tone of 132 kHz terminated by a brief FM sweep (Neuweiler *et al.* 1988). On the basis of these findings I conclude that the tiny eyes of echolocating bats such as *H. speoris* and *H. bicolor* are not efficient in prey capture, and may act as photoreceptors for 'sampling light' recurrently every 24 hours, thus entraining their circadian clocks. Similar views have been expressed by other bat researchers (Kunz 1982).

Mother-infant relations in *Hipposideros speoris*: Bats are altricial, with newborn pups being highly dependent on the mother. Females lavish a lot of attention on their young. *H. speoris* mothers either left their young behind in a crèche in the cave or carried them to the foraging areas. At first it appeared that there was no correlation between the age of the young and the frequency with which it got carried around by the mother (Marimuthu 1988). A more detailed subsequent study in our laboratory and statistical analysis (Kolmogrov Smirnov test, $p = 0.05$) on the patterns of mothers: i) carrying their young and ii) leaving them behind as a function of the size/age of the young, revealed that the two distributions (Fig. 22) differ significantly and that more bat pups are left behind as they become larger (Radhamani *et al.*1990).

The young that were left behind in the cave clung on all fours to the ceiling and scarcely moved. The mothers often returned before midnight and retrieved them. During retrieval, the mother moved towards her infant, gently touched it with her forearm and presented her ventral surface, especially the pubic region, moving in such a way that the young could hold on to the dugs with its teeth. Then the infant bat let go of its perch on the rock ceiling, nestled under the wing membrane of the mother, and oriented towards the mammary glands to suckle. When satiated, the young fluttered its wings and often hung from the neck of the mother. During the day the volant young bats routinely hung from the necks of the mothers and as the observer moved closer, they briefly flew away, to reunite with the mother and assume the same posture in 10 to 15 minutes (Marimuthu 1988). In this posture, the young have been seen to stretch their wings and simulate flight. I am not sure if any other species of Microchiropteran bat infants, in the tropics or temperate climes, use their mother's neck as a perch.

Marimuthu (1988) has also reported, from experiments performed under natural conditions and under semi-natural conditions in the outdoor

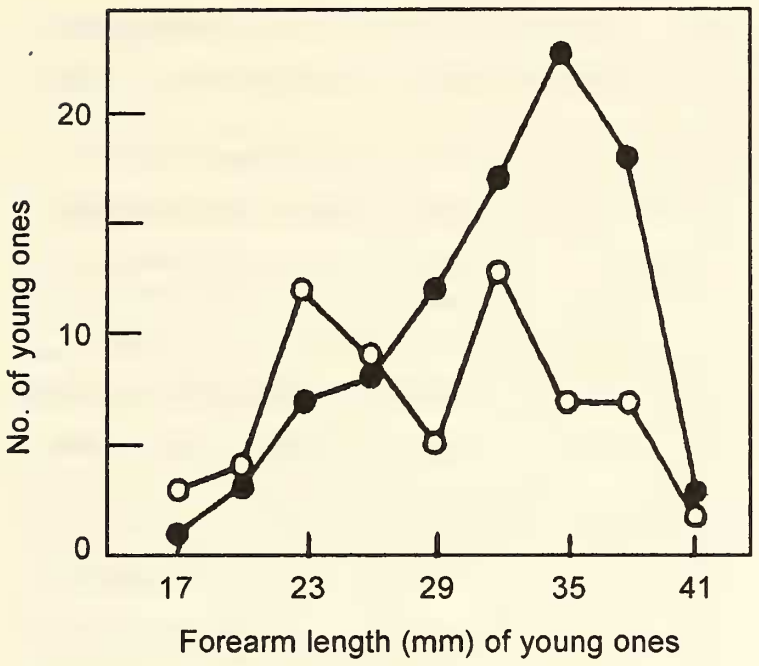


Fig. 22: The pattern of mother bats carrying their young (hollow circles) to the foraging areas, or leaving them behind in the cave (filled circles) as a function of the size (which corresponds to age) of the infants (After Radhamani *et al.* 1990)

bat enclosure, that female *Hipposideros speoris* identify their own pups. In an experiment performed close to the mouth of the Jain Hills cave, he placed six pre-volant pups on a cool rock. Mother bats returned in the pre-dawn hours and exhibited hovering and circling flight and possibly emitted trains of ultrasonic pulses of 134 kHz directed at the pups. The pups became agitated as though they were responding to the hovering mother bat, and raised their heads and emitted audible multi-harmonic squeaks (Habersetzer and Marimuthu 1986). Infant vocalisations attracted the mothers, who flew towards them and alighted close to them. The pups tried to cling to *any* bat mother but the mother bats snuggled closer and retrieved their own young. Mothers located their infants even when the juveniles were displaced from where the mothers left them. Behavioural experiments under both natural and captive conditions showed that the sound emission of the pups attract the mothers, but may not contain sufficient clues for them to correctly identify their own from among a group of squeaking young ones. The nuzzling of the mother among the pups is indicative that olfactory means also mediate final identification and retrieval (Gustin and McCracken 1987, Habersetzer and Marimuthu 1986, Marimuthu 1988). On many occasions I had observed infants of *Rhinopoma hardwickei* and *H. speoris* fall to the ground and emit faint but audible vocalisations, to be retrieved by obviously their own mothers. So there can be no doubt that vocalisations are the primary cue for infant recognition. Isaac and Marimuthu (1993b) have reported their accidental discovery of how a mother pygmy bat *Pipistrellus mimus* responded to the vocalisations of a one day old infant. A maternity colony of *Pipistrellus mimus* roosted for several years in a sleeve-like tunnel 1.3 m wide, 0.85 m high and 24 m long with a right-angled bend and just one entrance on the western side of the Department of Animal Behaviour and Physiology building. A small colony of 18 *Rhinopoma hardwickei* had also chosen this tunnel as a daytime roost. Suthaakar Isaac separated a one day old infant bat from its pipistrelle mother after tagging her, and took the infant to his work bench nearly 70 m away from where the mother bat was roosting on all fours. *Pipistrellus* spp. never carry their young to foraging grounds. The infant separated from its mother was emitting ultrasonic distress and isolation calls continuously, in the range of 30 to 80 kHz measured using a Mini-2 bat detector (Ultrasound Advice, UK). The time of day was 1800 hrs to 1900 hrs when the sun sets and bat colonies stir out. The mother was apparently flying around, heard the isolation calls of her infant and in response flew into the room through an open window and alighted on the infant, covered it with her wings, lifted it up and flew away. The entire rescue operation apparently lasted only a few seconds (Isaac and Marimuthu 1993b). Other researchers have also reported that bat mothers respond to calls of their own young (Balcombe 1990).

We commented in one of our papers (Radhamani *et al.* 1990), "The present study deals with mother-young relations in a cave-dwelling

insectivorous bat *Hipposideros speoris* and explains how the mother bats carry even their volant young to their foraging areas in order *to acquaint them* with the topography and foraging strategies", and later in the same report, "...more young ones are left inside the cave as they become larger". These two statements make, in fact, contradictory claims. Though volant subadult *H. speoris* can produce and hear CF/FM sounds (127-138 kHz) (Habersetzer and Marimuthu 1986) in the adult range, they face *opposite* the direction of the flight path of the mother while being carried. Subadult *Hipposideros* may use ultrasonics to form an acoustic picture of the interior of the cave and the immediate environment (Marimuthu 1988). In the case of *Megaderma lyra*, the mothers even carry infants which are nearly their own size. These bats are known to have secondary night time roosts. In Madurai, many of the *M. lyra* bat mothers used a cowshed as a night time roost and left their infants on the ceiling.

Breeding pattern of *Hipposideros speoris*: Brosset (1962a) writes of the breeding pattern of *H. speoris* of the Poona/Khandala region "The periodicity is absolutely strict for this species, and all females deliver together in May. The first to do so were observed around 5th May, and the last around the 25th of the same month". In Madurai, there are two peaks of breeding in *H. speoris*, the first and less pronounced peak in May and the second in November, which is how Radhamani (Radhamani *et al.* 1990) could make her observations on *Hipposideros* mothers carrying infants from August to December 1989. G. Marimuthu's detailed work on mother-infant interactions in this hipposiderid bat are based on observations made from December 1977 to February 1979 and November 1980 to February 1981 (Marimuthu 1988). Since a single young is the rule for most species of bats, we can only conclude that there are female *H. speoris* that bear young ones around May and other females that bear young around September/October. Almost all species of bats studied by Brosset (1962a, b, c, 1963) had a very narrow period of parturition. This is also the case in Madurai in the breeding pattern of *Hipposideros bicolor*, which often shared the same cave as *H. speoris*. All young of *Hipposideros bicolor* were born in May. The May peak is the typical breeding pattern to the north of the equator, and the November peak to south of the equator. Professor Aschoff (1913-1998) in personal conversations had often told me that he believed that the "biological equator" might be around eight degrees north of the geographical equator. Madurai interestingly is 9° 58' north of the equator.

Breeding pattern of *Pipistrellus mimus*: The vespertilionid bat, *Pipistrellus mimus* Wroughton, is a commonly occurring and widely distributed bat in India, except in mountainous regions. It is physically the smallest species of bats of India. It is eclectic in the choice of roost sites and lives inside caves, even in small depressions in rocks, cracks, crevices, buildings, inside thatches, tree holes and even in letterboxes. Adults weigh 3.9 ±0.4 gm (n=19) and the forearm measures 27.6 ±1.1 mm (n=26). A group of 20 members of *P. mimus* colonised the tunnel in our departmental building described earlier. Adult females and infants roost in groups, and adult males roost singly throughout the length of the tunnel. The study was carried out over one whole year, from May 1990 to May 1991. Observations were made during the day as well as the night, using a torch light with a red filter (>610 nm). The reproductive condition of every female was noted at each observation. In pregnant females, the embryo was detected by palpation and lactating females were easily identified by the presence of well-developed mammary glands. The young were also tagged. Infants with fresh umbilical cords were noted as being one day old. The time interval between the first parturition in the batch until the last parturition denotes a *cycle*

of breeding, somewhat confusingly called breeding "season" in our publication (Isaac *et al.* 1994).

Gopalakrishna *et al.* (1975) reported that *Pipistrellus mimus* was a "continuous breeder". Suthaakar Isaac, a Ph.D. student of G. Marimuthu, studied the breeding patterns of this vespertilionid as a part of his research programme. It soon became apparent that parturition in this bat occurs in four distinct and discrete cycles in a year as shown in Fig. 23. The first cycle of breeding lasted from July 5-14, 1990 (n=6); the second cycle lasted from September 14 to October 30, 1990 (n=8); the third cycle lasted from December 21, 1990 to February 23, 1991 (n=8); the fourth cycle lasted from March 23 to April 11, 1991 (n=3) (Isaac *et al.* 1994). *P. mimus*, unlike other microchiropteran bats of southern India, gave birth to twins. Females gave first birth to twins at the minimal age of 103 days. Possibly facing high mortality rates, this bat species would have to increase the rate of reproduction. Dead infants were often seen on the floor below the daytime roosts of this bat. Since the mother bat does not carry her young, the rate of predation at the roost may also be higher than that in other bats. It is also a behavioural oddity that *P. mimus* bats are the earliest to fly about at dusk, and the last to return to the roost at dawn, thus exposing themselves twice in 24 hours to visual detection by predators (Isaac and Marimuthu 1993a) such as the black-shouldered kite *Elanus caeruleus*. Their flight activity pattern is crepuscular. We have, however, never witnessed any birds of prey capture a bat. We have confirmed that the same female bats underwent successive pregnancies and parturitions. Our results imply that *P. mimus* is the most prolific breeder among the microchiroptera. It would be interesting if similar studies as ours (Isaac *et al.* 1994) are undertaken for other organisms that are often claimed to be "breeding continuously in the tropics."

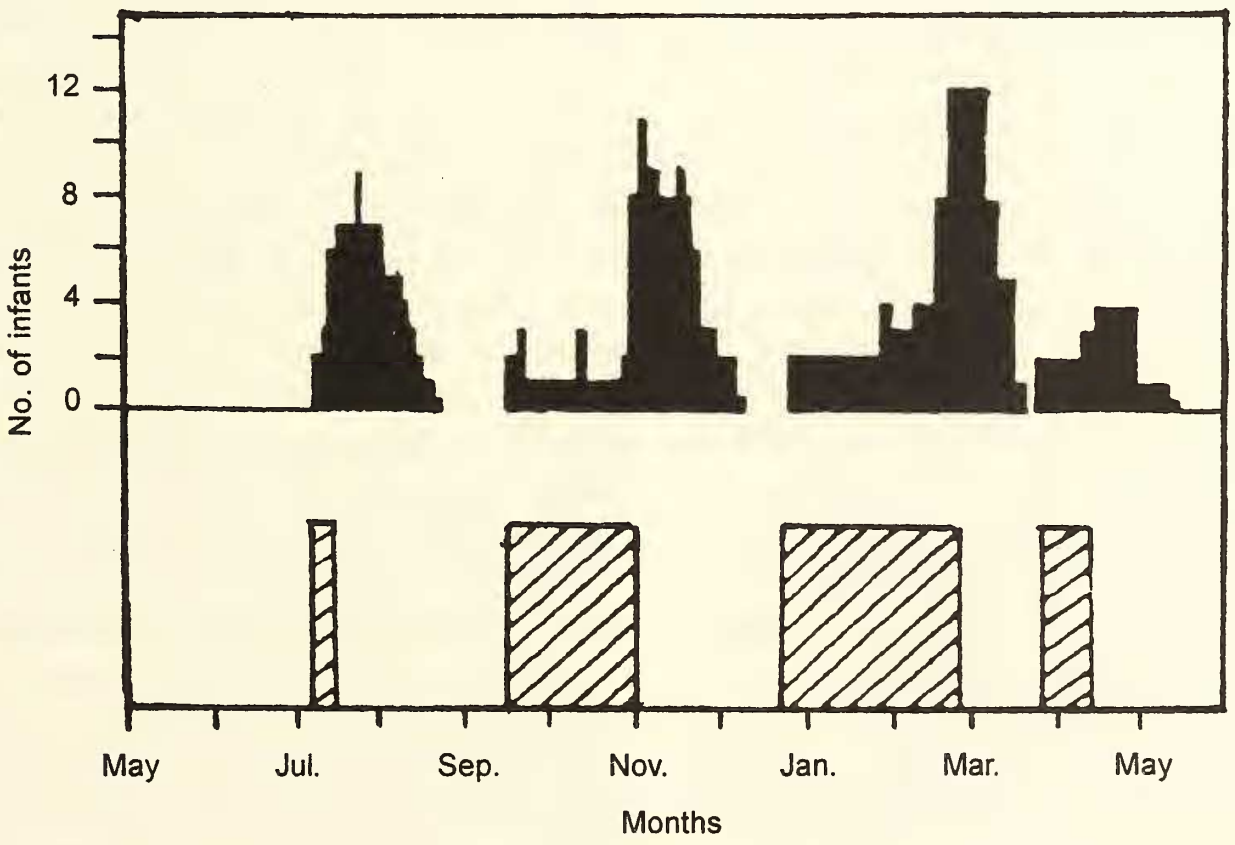


Fig. 23: The four breeding seasons of *Pipistrellus mimus*.
The upper panel represents number of infants from newborn to pre-volant stages, found in the tunnel.
The striped areas in the lower panel indicate durations of parturition (After Isaac *et al.* 1994)

General Remarks

Personally for me, there remain many unsolved puzzles in the bats I studied. Inside the cave of Jain Hills I noticed, at around 1400 hrs to 1600 hrs, how still the colony of *Hipposideros speoris* became. No bats flew around, even the restless circular movements of the heads of the bats had substantially abated, and it looked as though the bats were indeed in deep sleep. At such times if my movements happened to cause the slightest displacement of a smooth pebble under my feet, the ensuing muffled noise made a hundred bats jerk up in alarm. This 'alertness in sleep' is perhaps an adaptation against predators like the smoothly gliding snakes. Dilip Joshi often brought to the laboratory the sloughed skin of big snakes, which he found inside the cave. The cave was also visited by bandicoots, and we had lost at least one experimental male *H. speoris* to these nightly predators. There were also barn owls and owlets at the cave mouth. I had on one occasion, during our field ethology work on foraging, noticed what might have been a barn owl, capturing a bat. Interestingly, the same *H. speoris* bats, ultra-sensitive to small noises within the cave, flew later in the night around 2000 hrs in the central bus stop of Madurai or in the noisy railway station. The hissing of the engines and the throngs of passengers did not appear to bother the hunting hipposiderid bats. This suggests that there is a heightened threshold sensitivity to audible sound when bats are on the wing. This may also explain why the 'best hearing frequencies' of insectivorous bats have such a restricted band, often excluding sounds audible to humans. Similarly these shy creatures, which avoid the brightness of the sky on full moon nights and fly under canopy cover, forage on swarms of insects drawn to bright sodium-vapour streetlights.

All the species of insect bats that we examined showed roost fidelity, with the exception of *Tadarida aegyptiaca* (body weight 22 to 24 g). This bat is a strong flier that preferably forages at considerable heights of 15 to 20 m above the ground, well over the canopy and ponds. A colony of *c.* 2,000 bats lived in crevices and cracks of a vertical rock on the northern slope of the Jain Hills. They were very noisy, squeaking in chorus, a little before the onset of the evening foraging flight and were difficult to observe. We had planned to monitor activity/rest patterns of this bat also, but were surprised, when we arrived at the site of the colony one evening not a single bat was to be seen. No other bat colony in the Madurai region had vacated its roosting site as *T. aegyptiaca* did. A few weeks later we were informed that some bats had returned. In view of the inconvenience involved in studying the behaviour of this bat roosting in the narrow crevices of the rock at a height of 50 to 70 m, we decided not to continue with our observations on *T. aegyptiaca.*

I have left out much of our laboratory experimental findings on light-induced PRCs made for the circadian rhythms of *Taphozous melanopogon,* and *T. kachhensis* and *H. speoris* to avoid unnecessary technical details. We had reported that the circadian rhythm in activity-rest cycles free-runs in dim light of 5 lux and responds to dark breaks of 2 hours and 4 hours, with advance and delay phase shifts as a function of phase experiencing the 'blackout'. Similarly, phase shifts are also caused by light pulses of 15 minutes and 1000 lux given at different phases. We reported for the first time for any model system (Subbaraj and Chandrashekaran 1978), that the time course and waveform of phase response curves obtained from experiments using pulsed light and pulsed darkness are mirror images of each other. The idea of reviewing our studies was to impart a flavour of the kind of work my students and I had been doing on insectivorous bats, among other objects, at the MKU for two decades. Many of the observations reported here were also first reports of their kind, when they were made. The ecology of roosting sites, site

fidelity and social interactions of some of these bats were the most fascinating facets for me.

ACKNOWLEDGEMENTS

The kind of research described here could not have been carried out without the enthusiastic participation of venturesome students like R. Subbaraj, G. Marimuthu, K. Sripathi, Dilip Joshi and K. Usman. I thank Dhanashree Paranjpe for helping me with the figures. I thank Professor Hubert Markl for encouragement and the gift of a jeep, when he was Vice-President of the Deutsche Forschungsgemeinschaft, which enabled more comfortable travel and transport of some equipment to rugged cave sites. The Alexander von Humboldt-Stiftung donated equipment and the UGC, DAAD, DFG and the Alexander von Humboldt-Stiftung enabled me to visit universities in Germany for six weeks every year between 1979 and 1991. The UGC, CSIR and DST financially supported my researches at the MKU, while its School of Biological Sciences, thanks to its founder Professor S. Krishnaswamy (1926-1988), became a supportive environment for teaching, thought and exciting experiments for two decades. I thank an unknown referee for suggesting changes that improved readability considerably in the final version of this manuscript.

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Appendix I: Breeding periodicity in the Madurai bats

Megaderma lyra	:	March/April/May.
Rhinopoma hardwickei	:	April & November.
Hipposideros speoris	:	Through the year with a November peak.
Hipposideros bicolor	:	April/May.
Taphozous melanopogon	:	April.
Taphozous nudiventris kachhensis	:	October.
Cynopterus sphinx	:	March/April/May/June/July.
Rousettus leschenaulti	:	March/April/May/June/July.
Pipistrellus mimus	:	First cycle: July 5-14, 1990 (n=6); second cycle: September 14 to October 30, 1990 (n=8); third cycle: December 21, 1990 to February 23, 1991 (n =8); fourth cycle: March 23 to April 11, 1991 (n=3) (Isaac *et al.* 1994).

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